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# The cytology of *Vaucheria*

CATHERINE GROSS

(WITH 31 FIGURES)

*Vaucheria* has been the object of much study since the genus was first described by Vaucher (1803). Most attention has been devoted to the development of the sexual organs. Nägeli (1847), Pringsheim (1855), De Bary (1866), Schmitz (1879), Berthold (1881), Behrens (1890), and others have described oögenesis and spermatogenesis as observed in living material or in filaments stained *in toto*. Oltmanns (1895) used the paraffin method in conjunction with the study of living material in *V. clavata*, *V. fluitans*, and *V. Eveisa*. According to his description, after the oögonium reaches its full size there is a migration of material from the oögonium into the parent filament. This *Wanderplasm* includes some cytoplasm, a few chloroplasts, and all the nuclei but one of the young oögonium. Soon after this migration a cross wall cuts off the now uninucleate oögonium. Heider (1908), studying *V. pachyderma*, *V. arrhyncha*, *V. geminata* and *V. dichotoma*, and Couch (1932), studying *V. sessilis*, *V. geminata*, *V. pachyderma* and *V. aversa*, have confirmed Oltmanns' description. Davis (1904), however, described a different fate of the supernumerary nuclei in the oögonium of *V. geminata racemosa*. He saw no evidence of nuclear migration; on the contrary a degeneration of nuclei begins in the young oögonium a little before the formation of the cross wall and continues after this wall has completely separated the oögonium. In consequence, the mature oögonium retains but one nucleus which functions as the egg nucleus. Miss Williams (1926) and Mundie (1929), both studying *V. geminata*, have confirmed Davis' account of the degeneration of the supernumerary nuclei after the formation of the oögonial wall.

Few references appear in the literature to the cytology of the vegetative structures of *Vaucheria*. Kurssanow (1911) described mitotic figures in *V. terrestris*, *V. uncinata*, and *V. repens*, and Hanatschek (1932) has corroborated and extended this work on *V. sessilis*.

## MATERIAL AND METHODS

*Vaucheria sessilis* (Vauch.) DC. has been found fruiting in abundance about the first of October on moist rocks in a pool in the botanical greenhouses of the University of Wisconsin. *V. geminata* (Vauch.) DC. fruits in the same location most abundantly about the first of November. *V. geminata* soon outgrows *V. sessilis*, which disappears until the following spring.

Each autumn and spring from 1931 to 1935 fixations were made of both these species. Small amounts of the material were fixed hourly during a period of twenty-four hours. Of the fixing fluids employed, chrom-acetic acid (1 g. chromic acid, 1 cc. glacial acetic acid, 100 cc. distilled water) proved most satisfactory, causing no serious shrinkage of cellular structures. After imbedding in paraffin, sections were cut  $6\mu$  to  $8\mu$  in thickness. Flemming's triple stain was used chiefly; Newton's crystal violet-iodine method was also very satisfactory. The best results with the triple stain are obtained by overstaining in crystal violet. The chloroplasts are then a pale pink, in contrast to the deep blue of the nuclear material.

Living plants of *V. sessilis* and *V. geminata* were observed also in conjunction with the sectioned material. For the study of this material in a living condition, a  $3\times 1$  inch cover slip was fastened parallel to and about a quarter of an inch from a glass slide. Between cover slip and slide was placed a small amount of water in which was a filament already showing evidence of forming an antheridial stalk. If uninjured, such a filament grows rapidly and produces the sexual organs. Growth was studied under a  $44\times$  objective and a  $5\times$  ocular. The sex organs abort readily, and often their production ceases when the plant is injured in any way; consequently no method of studying the living material was always successful. However, on many occasions it was possible to trace the development of individual oogonia and antheridia to maturity.

Studies were also made of material fixed hourly in formol-acetic-alcohol, stained with Heidenhain's iron-alum haematoxylin and mounted *in toto* in Venetian turpentine.

#### OBSERVATIONS

*Mitosis.* Mitoses have been studied in the vegetative and antheridial filaments of *Vaucheria geminata*, the divisions being essentially similar in both. Division figures were most abundant in material fixed about midnight; however, all stages of division may be found at any hour. A typical resting nucleus (fig. 1) is approximately spherical, varying in diameter from  $3\mu$  to  $5\mu$ . It has a membrane, a large, spherical, deeply staining nucleolus, and a faintly staining chromatic material in granular rather than in reticulate form. This observation agrees with that of Kurssanow (1911) who found the chromatic material reticulately arranged in the larger nuclei, but granular in the smaller ones. According to Hanatschek (1932), however, there is a deeply staining intranuclear body which divides, one half going to each pole of the achromatic structure to form a centrosome-like body.

As the nucleus increases in size, the chromatic material collects in the peripheral region, now retaining more of the violet stain than previously.

The nucleolus becomes more or less jagged, radiations connecting it to the peripheral chromatic substance (fig. 2). A spireme is gradually formed, at first rough but gradually becoming smooth (figs. 3, 4). The spireme stage is very seldom seen and it may be assumed that it is passed through quickly. The most common mitotic figure is that of a somewhat later stage at which numerous strongly stained, apparently unconnected, bodies are visible (fig. 5).

At the stage shown in figure 5, the nucleolus, which has been diminishing in size has usually disappeared. The chromatic bodies become fewer, perhaps in consequence of fusion, until about seven can be counted (fig. 6). Hanatschek (1932) described seven to ten such bodies in *V. sessilis* and Mundie (1929) counted five in *V. geminata*. Apparently these bodies are chromosomes; however, the number was not definitely established as constant. The nucleus now becomes slightly pointed (fig. 7), one pole being slightly retarded in its formation; however, the whole nucleus soon becomes spindle-shaped. Fibers appear within the nuclear membrane and the chromosomes become arranged in an equatorial position (fig. 8). I have seen no centrosome-like structures, possibly because the triple stain was used. Such a body at each pole of the spindle has been described by Kursanow (1911) and Hanatschek (1932), in material stained with haematoxylin.

Later (fig. 9), the daughter chromosomes separate and are pulled to the poles. During the anaphases it is difficult to distinguish individual chromosomes (figs. 9, 10). These chromatic masses appear to push out of the membrane of the mother nucleus (fig. 10). Later, small chromatic bodies appear and a nuclear membrane is visible about each daughter nucleus (fig. 11). The old nuclear membrane is still visible connecting the daughter nuclei. In each of the latter a nucleolus appears and a spireme is formed. The daughter nuclei separate, stretching the parent nuclear membrane, and, even when the daughter nuclei have reached a distance of  $10\mu$ , the old membrane is still visible (fig. 12). When the mother membrane at last disappears, the typical resting nuclear structure is visible (fig. 1).

*Development of sex organs in V. sessilis.* On many occasions the development of an oögonium and of an antheridium was followed from the beginning of the protrusion of the antheridial stalk to the completion of syngamy. Pringsheim's (1855) description of the formation of the sexual organs has been altered little by more recent workers. Oltmanns (1895) first noticed a daily rhythm in the development of the sexual organs. I have observed, in general, this rhythm in *V. sessilis*; however, any stage in the development of a sex organ may be found at least occasionally any time of day. The time relations noted in one series of observations of an antheridium and oögonium is shown in table 1.

An antheridial branch first appears as a slight protuberance on the side of a vegetative filament. At the base of the protuberance is an accumulation of dense cytoplasm, chlorophyll and oil drops. At the extremity of this accumulation, next the filament wall, is always a thick layer of dense cytoplasm.

The terminal portion of the branch begins to curve early in its development. Not all the chloroplasts and oil drops are carried out into the branch with the rest of the cytoplasm, so that, as its growth continues, the branch becomes a lighter green than the main filament; in the curved portion it is practically colorless. In this portion there is now visible in the living condition a movement in all directions. Small vacuoles in the end of the

TABLE 1  
*Development of sex organs in V. sessilis*

		ANTHERIDIUM	OÖGONIUM
Nov. 26, 1932			
7	P.M.	Beginning of protrusion	
6	A.M.	Beginning of hook	Beginning of protrusion
12	M.	Cell division separating antheridium and stalk	Beak present
Nov. 28			
1	A.M.		Wall completed separating oögonium from parent filament
1:45	A.M.		Beak opened
2	A.M.	Antherozoids released	
2:15	A.M.	Antherozoid enters egg	
3	A.M.		Beak closed
Nov. 30			Thick wall layer formed within oögonial wall

branch coalesce, forming several larger ones. As the vacuoles grow, the movement appears to stop at the beginning of the curvature, the cytoplasm containing the chloroplasts thus being held back from the vacuolated region. Between the much-vacuolated cytoplasm and that containing the chloroplasts, cell division occurs and a wall is formed, separating the antheridium from its stalk. The method of cell division was not determined.

Soon the movement which had been noticed in the antheridium becomes concentrated in the vacuoles and becomes more vigorous. The antheridium swells, becomes turgid, and finally bursts, releasing motile antherozoids. No pore is formed. Not all the antherozoids escape at once. After the first sudden outburst two later escapes occur at intervals. An antherozoid after its release has a red pigment spot and two cilia. The exact attachment of the cilia could not be determined in *V. sessilis*.

The antherozoids are very active for about fifteen minutes; as their movement becomes slower they are attracted toward the beak of the oögonium. Many of them move in an amoeboid fashion over the surface of the oögonium. On several occasions an antherozoid was seen to pene-

trate the egg. The formation of antherozoids was not studied in section.

The oögonial branch originates in much the same way as the antheridial branch, but does not appear until the latter has begun to curve. The oögonial protuberance soon swells, taking on a globular form. There is a much greater inflow of material into the protuberance than into the antheridial branch. The beak appears after about six hours and is the point in the protuberance toward which movement is directed. Oil moves into the oögonium in large quantities. Only the beak remains hyaline. After the beak is formed a large vacuole appears in the center of the oögonium traversed by cytoplasmic strands. Chloroplasts and oil drops appear in the cytoplasmic strands and in great abundance in the peripheral portion of the oögonium.

Occasionally, in 1931, material to be studied during a period of several days was removed from its normal habitat and placed in Petri dishes. Usually, in this material, starting at the beak, a protoplasmic movement began which carried many of the chloroplasts toward the base of the oögonium. Here they remained for a time, and then the protoplasmic mass containing them passed out into the main filament where it soon became dispersed. Some of this material in which the protoplasmic movement, suggestive of Oltmanns' *Wanderplasm*, occurred was sectioned. It was difficult to obtain suitable sections through young oögonia; one section, however, did show this mass of *Wanderplasm* with its numerous chloroplasts and thirty nuclei (fig. 26). In the young oögonium there remained twenty nuclei. Whether most of these ultimately migrated or degenerated could not be determined. Within the last few years a pool in the university greenhouse has provided excellent material, and filaments for the study of living material have been taken directly from the pool. In this material no protoplasmic movement backward from the oögonial branch has ever been observed in either living or sectioned material (fig. 25). Mounts in Venetian turpentine of material fixed directly from the normal habitat, likewise show no evidence of a *Wanderplasm*.

Filaments of *Vaucheria* are extremely sensitive to any change in environment. It seems possible that a change in the habitat of the plant influences protoplasmic movement; any such movement would doubtless carry with it some chloroplasts, nuclei and other inclusions. In *V. sessilis* it appears from my study that a degeneration of the supernumerary nuclei in the oögonium takes place, but that under certain environmental influences there is a migratory plasma which may carry with it some or all of the nuclei. Davis (1904), Miss Williams (1926), and Mundie (1929), using material fixed directly from the normal habitat, described a degeneration of the nuclei in the oögonium. Oltmanns (1895), Heidinger (1908) and Couch (1932) collected material and placed it in Petri dishes



for study over a period of several days or weeks before fixation. These authors described a *Wanderplasm*. The suggestion is strong that the movement of a *Wanderplasm*, carrying nuclei backward from the oögonial branch, is a response to non-natural conditions.

A series of small vacuoles at the base of the oögonium begin to flatten and fuse to form larger ones. Fusion continues until there is one large flattened vacuole extending across the base of the oögonium, its edges touching the plasma membrane, and thus completing cell division. There are no cleavage furrows extending out from the plasma membrane to meet the membrane of the vacuole. Between the two portions of the flattened vacuolar membrane, now very close together, a cross wall is formed between the oögonium and the main filament. This method of wall formation is suggestive of that described by Harper (1899) for columella-formation in the sporangiophore of *Sporodinia*.

After the oögonium is thus separated from the parent filament, the chloroplasts and oil drops within the oögonium move toward its base and become hexagonal, suggesting the effect of considerable pressure. The beak now contains a colorless mass of cytoplasm, over which the wall of the oögonium is noticeably thinner than elsewhere. Suddenly the wall of the beak bursts and most of the colorless mass is extruded. At about the same time the antherozoids are released from the antheridium, swim about, and fertilization occurs. This description of fertilization is very similar to that given by Pringsheim (1855) and other workers; however, Dippel (1856) and Nägeli (1847) thought that the antheridium fuses with the beak of the oögonium and that the contents of the former pass into the latter, as in *Zygnemaceae*. The contents of the antheridium are not usually expelled toward the oögonium but in the opposite direction, the antherozoids, not the antheridium itself, then, being attracted to the beak opening. In many instances the antheridium has burst and the antherozoids have disappeared before the oögonium is mature. Whether or not an antherozoid enters an egg, a thick wall is formed inside the oögonial wall several days after the contents of the beak have been extruded. A thick-walled oögonium with one nucleus is often seen. In such a case, the egg has formed a thick-walled spore without any gametic union. Attempts to germinate such spores were unsuccessful.

*Development of sex organs in V. geminata.* The sexual branch of *V. geminata* makes its appearance in much the same way as does that of *V. sessilis*. Because of the form of this branch, with its twisted antheridium and bent oögonial stalks, it is almost impossible to follow its development in the living condition after the early stages. In the study of living material no movement of any kind was seen which might indicate a migration from the oögonium back to the parent filament. Sections through young

oögonia also give no indication of nuclear migration. Figure 21 shows a section through a young oögonium at the base of which is a large vacuole. This is the condition just previous to the formation of the cross wall. More than fifty nuclei are present in the oögonium; these stain less readily than do the nuclei of the surrounding filaments. The nuclear membranes are no longer distinct; the nucleoli, however, are persistent. One oögonial nucleus (not shown in figure 21) remains in a typical vegetative state, retaining a definite membrane. This nucleus lies near the point at which the beak is to form. Soon all the nuclei except this one disappear entirely; darkly staining bodies, however, appear at about the same time. The persistent nucleus near the beak increases somewhat in size; it is now surrounded by a small mass of cytoplasm with radiating strands (fig. 22). Conditions like those in figure 21 suggest that the cross wall is to be formed before fertilization. The study of living material, as well as of sectioned material, also shows that a cross wall is formed before the beak opens, and hence before fertilization can occur. This is contrary to the description of Mundie (1929), according to whom, fertilization occurs before cell division separates the oögonium from the parent filament.

The antheridium is formed in a manner very similar to that described for *V. sessilis*. The opening through which the antherozoids are released is a definite pore. The antherozoids (fig. 20) are somewhat larger than those of *V. sessilis*. Each has a red pigment spot and two cilia apparently of equal length attached toward the anterior end. All the antherozoids are freed at the same time, but some of them remain non-motile and without cilia, embedded in a gelatinous substance. The latter mass may be found in the same condition several hours after fertilization has taken place. As antherozoids were seen on only two occasions this extrusion in a non-motile condition may not be typical. The ciliated antherozoids are active for a very short time.

It is impossible to determine whether all the eggs in the oögonia on a single sexual branch are fertilized; however, after the beak of an oögonium is opened, in a manner similar to that described for *V. sessilis*, one or two antherozoids may be seen swimming into the opening. Sectioned material shows that an antherozoid nucleus, increasing in size, migrates toward the cytoplasmic mass in which the female gamete lies. Both nuclei come to lie side by side in this star-shaped mass (fig. 23). In the cytoplasmic strands of the oögonium fiber-like structures now appear which stain dark blue. Although scarcely visible before the fusion of the egg and antherozoid nuclei, these fibers become more evident as the zygote matures. The chloroplasts in the crystal violet-iodine stain are blue, the nuclei and the smaller cytoplasmic bodies retaining more of the violet. With Flemming's triple stain the chloroplasts are pink.

As the zygote matures, the two gamete nuclei move to a more central position and increase in size (fig. 24). Both appear very similar, each having a large nucleolus and a chromatic network (fig. 13). The two nuclei come to lie so close together that it is difficult to distinguish them. The cytoplasmic mass in which they are embedded retains at first much of the safranin of the triple stain; later, more of the crystal violet (fig. 27). In only a few oögonia examined was it possible to see details of the fusion nucleus. Fourteen darkly stained bodies were discernible in such instances against a very dense, homogeneous background (fig. 19). These fourteen bodies may represent the diploid number of chromosomes, since seven was the most common number of chromosomes seen in the vegetative nuclei. Nuclear fusion evidently occurs in this cytoplasmic mass, for a larger nucleus soon appears with a definite reticulum bearing many granules (figs. 14, 29). No nucleoli are at first visible; but, as the granules on the reticulum disappear, a large nucleolus appears (fig. 15). As the zygote nucleus grows there is an accumulation of very homogeneous dense cytoplasm in the central part of the zygote. Outside this accumulation are bodies which stain a deep red. These are smaller than the chloroplasts in the vegetative filaments, but apparently are transformed or modified chloroplasts. In the much-vacuolated peripheral cytoplasm is a very evident blue-staining fibrillar substance. The zygote nucleus always lies next to the central mass, but not in it.

The nucleus increases in size (fig. 16), the reticulum stains more darkly, chromatic knots appear and a spireme becomes visible (fig. 17). Two nucleoli appear (fig. 18), and later four (fig. 28). The actual division of the zygote nucleus was not seen. At later stages, however, two nuclei are present (fig. 30); later four are seen (fig. 31), each containing a nucleolus and a chromatic network. Two nuclear divisions, probably the meiotic divisions, occur therefore in the zygote. Heidinger (1908) and Davis (1904) saw no nuclear divisions in the oögonium, hence meiosis can not occur in the formation of the female gamete. I was never able to find mitotic figures in the oögonium, although the nuclei in the antheridium may undergo typical somatic divisions. Miss Williams (1926) assumed from the formation of four nuclei that reduction occurs in the zygote. Hanatschek (1932) on the basis of certain stages resembling those of meiosis, came to a similar conclusion. Mundie (1929) alone, on the basis of a reduced number of chromosomes, has described meiosis as occurring in the formation of gametes.

The division of the zygote nucleus occurs many months before a germ tube is produced. Some zygotes, formed at the same time as those studied in section, did not produce germ tubes for four months and then a nutrient solution was used.

The writer is indebted to Dr. C. E. Allen for advice and encouragement during the course of this study, which was undertaken at his suggestion and carried out under his direction in the Department of Botany of the University of Wisconsin.

#### SUMMARY

1. The vegetative nuclei of *Vaucheria geminata* undergo a mitotic division similar to that described by Hanatschek and Kurssanow for other species of *Vaucheria*.

2. Observations on the development of the sexual organs in some living material of *V. sessilis* corroborate those of Pringsheim and Oltmanns; apparently, however, the appearance of a *Wanderplasm* is due to a change in environment and is not a typical occurrence. Study of living material and sectioned material shows no nuclear migration from the oögonium into the parent filament.

3. In living material of *V. geminata* also no cytoplasmic movement is demonstrable from the oögonium into the sexual branch. Sectioned material shows no nuclear migration from the oögonium. A degeneration of nuclei occurs within the oögonium after its separation by a cross wall from the sexual branch.

4. Fertilization occurs after the separation of the oögonium as a distinct cell. An antherozoid bears two equal cilia at its anterior end. The antherozoids of a given antheridium are released simultaneously through a terminal pore.

5. The zygote nucleus undergoes two divisions before a germ tube is produced. These divisions are probably meiotic.

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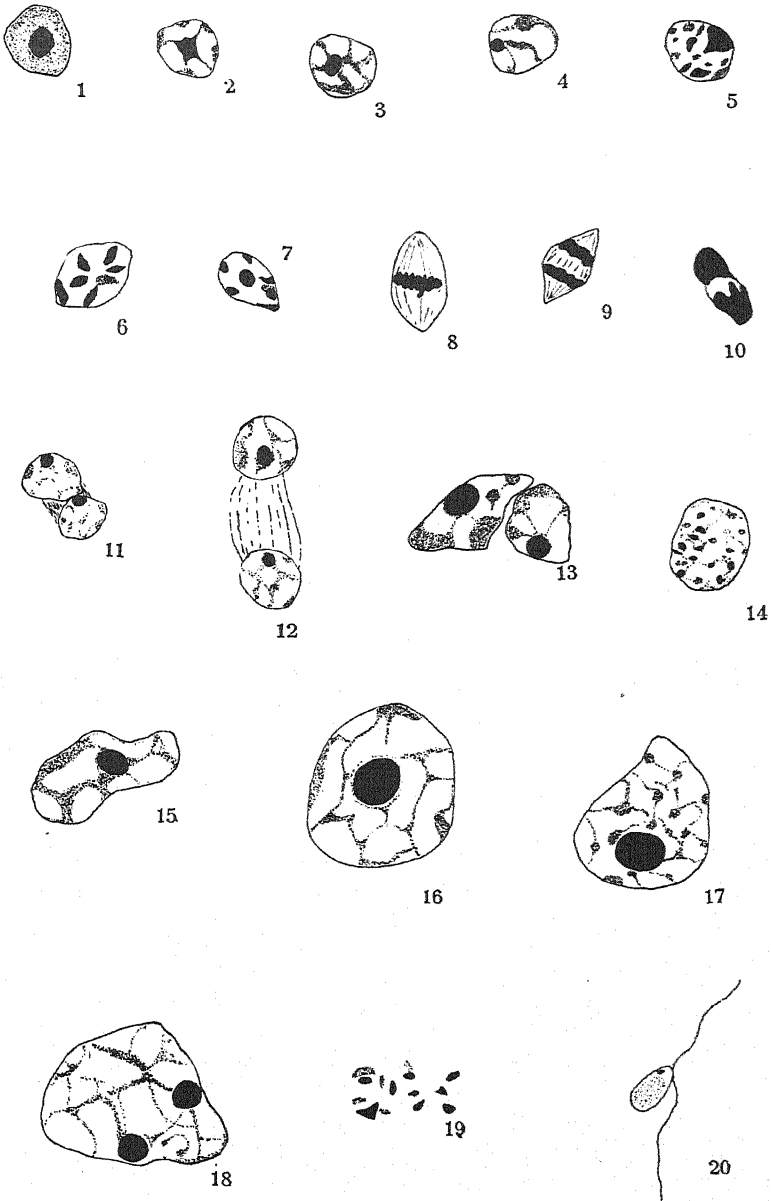
### Explanation of figures

All figures were sketched with an Abbé camera lucida. A Spencer 100× oil immersion objective, 5× and 10× oculars, and 20× and 25× compensation oculars were used.

Magnifications given allow for reduction in engraving. Figures 1-13 inclusive, and figures 15, 17, 18, and 19 are magnified about 2800 times. Figure 14 has a magnification of 1624 times, figures 16 a magnification of 3900 times, and figure 20 a magnification of 1500 times. Figures 21 to 31 inclusive are magnified about 812 times.

### Explanation of figures 1-20

- Fig. 1. A resting vegetative nucleus of *V. geminata*.
- Fig. 2. A vegetative nucleus preparing to divide.
- Fig. 3. Spireme formation.
- Fig. 4. Spireme present.
- Fig. 5. An early prophase.
- Fig. 6. A nucleus showing seven chromosomes.
- Fig. 7. A nucleus showing seven chromosomes; nucleolus still visible.
- Fig. 8. Equatorial-plate stage.
- Fig. 9. Early anaphase.
- Fig. 10. Late anaphase.
- Fig. 11. Two sister vegetative nuclei after the completion of mitosis.
- Fig. 12. Two sister vegetative nuclei with membrane of mother nucleus still visible.
- Fig. 13. The egg and antherozoid nuclei of Fig. 24 enlarged to show chromatic network.
- Fig. 14. Zygote nucleus.
- Fig. 15. Zygote nucleus with chromatic network.
- Fig. 16. Zygote nucleus after an increase in size.
- Fig. 17. Zygote nucleus; chromatic network becoming more dense and knotted.
- Fig. 18. Further development of the zygote nucleus; spireme.
- Fig. 19. Detail of fusion nucleus; fourteen bodies, probably chromosomes.
- Fig. 20. An antherozoid of *V. geminata*.



### Explanation of figures 21-26

Fig. 21. Longitudinal section of a young oögonium before fertilization; cross wall forming at the base of the oögonium; many nuclei in the process of degeneration.

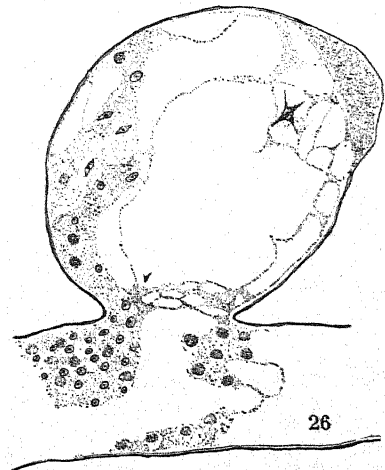
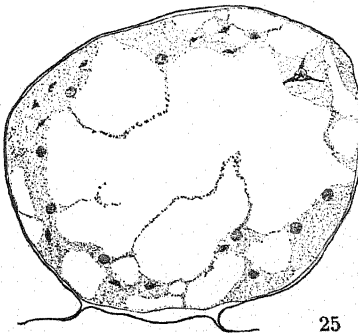
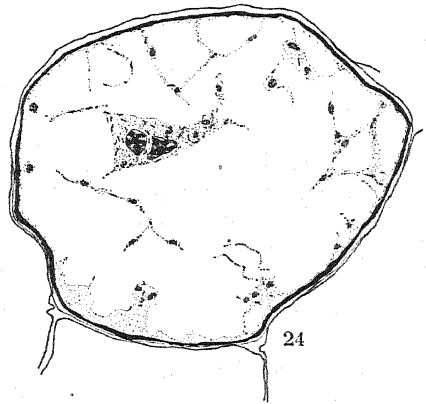
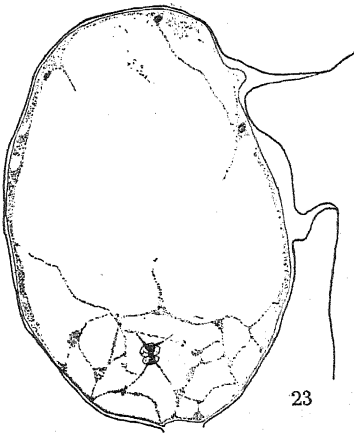
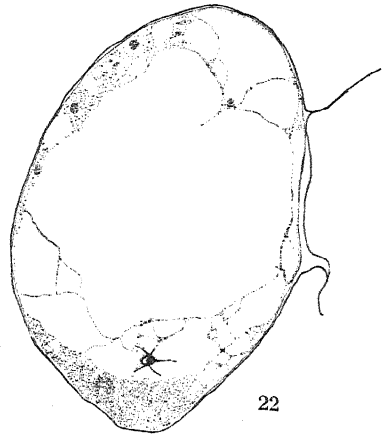
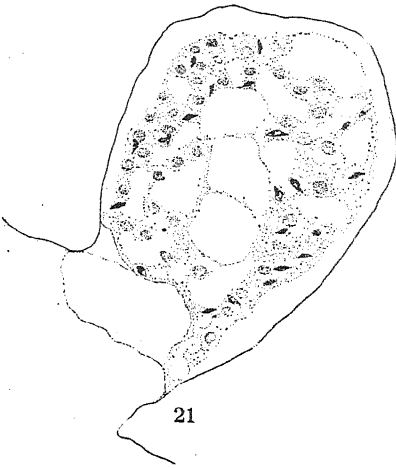
Fig. 22. Longitudinal section through an oögonium after the cross wall is completely formed; the egg nucleus in a star-shaped mass of cytoplasm.

Fig. 23. Longitudinal section through an oögonium; male and female nuclei just after entrance of an antherozoid.

Fig. 24. Longitudinal section through an oögonium; male and female gamete nuclei just before their fusion.

Fig. 25. Longitudinal section through an oögonium of *V. sessilis*; degeneration of all nuclei except the egg nucleus.

Fig. 26. Longitudinal section through an oögonium of *V. sessilis*; many nuclei just after being carried out of the oögonium by a cytoplasmic movement.





#### Explanation of figures 27-31

Fig. 27. Longitudinal section through a zygote of *V. geminata*, showing material in the center within which nuclear fusion takes place.

Fig. 28. Section through a mature zygote; the nucleus lies just outside the central homogeneous mass of cytoplasm in a more vacuolated region.

Fig. 29. Longitudinal section of the zygote showing the nucleus.

Fig. 30. Germinating zygote with two nuclei.

Fig. 31. Germinating zygote with four nuclei.

## Concerning the chromosome number of *Trautvetteria carolinensis*

SAMUEL LEWIS MEYER

*Trautvetteria carolinensis* is a monotypic genus of the family Ranunculaceae found in North America and eastern Asia. Its range has been described as extending from southwestern Pennsylvania to the mountains of Virginia and Kentucky, south to Florida, and west to Indiana and Missouri. The plant was named for Professor Ernst Randolph von Trautvetter, an able Russian botanist of the 19th century. The common name is "False Bugbane."

This ranunculaceous herb was first described by Walter (1788) and was called by him, *Hydrastis carolinensis*. Michaux (1803) described the same plant but called it *Cimicifuga palmata*. The generic name now in use was given by Fischer and Meyer (1834) when the plant was termed *Trautvetteria palmata*. Accepting this generic name and having cognizance of the priority of the specific name given by Walter, the plant was designated *Trautvetteria carolinensis* by Vail (1890). In discussing what he believed to be new species of the genus, the term *Trautvetteria applanata* was later used by Greene (1912).

During the summer of 1934, the suggestion was made to the writer by Dr. Ivey F. Lewis, Director of the Mountain Lake Biological Station of the University of Virginia, that it might be interesting to investigate certain of the anatomical features of this particular member of the Ranunculaceae. In looking through the literature pertaining to such a subject, it was observed that differing chromosome numbers had been reported for this monotypic genus.

Langlet (1927) reported the haploid chromosome number of *Trautvetteria carolinensis* as 14. Tischler (1931) gave this number as more than 24. Langlet (1932) pointed out that both his own previous report and that of Tischler were incorrect as he had found the somatic or diploid chromosome number to be 16. The present investigation was begun in order to correct, or verify, these observations.

The material used consisted of root tips collected from plants growing along the margin of Mud Branch, a small stream near the Mountain Lake Biological Station of the University of Virginia, Giles County, Virginia. The material collected in the summer of 1934 was fixed in Nawaschin's solution; that gathered in the summer of 1935 was fixed in Allen's B-15. The root tips were run through the usual paraffin technique, cut at 10 micra, and stained in iron-alum haematoxylin.

Studies were made of chromosomes at the metaphase of mitosis in

transverse sections of root tips. There were observed some incomplete chromosome plates in which there was a range of from 13 to 15 chromosomes. In the best plates, however, the number was very definitely

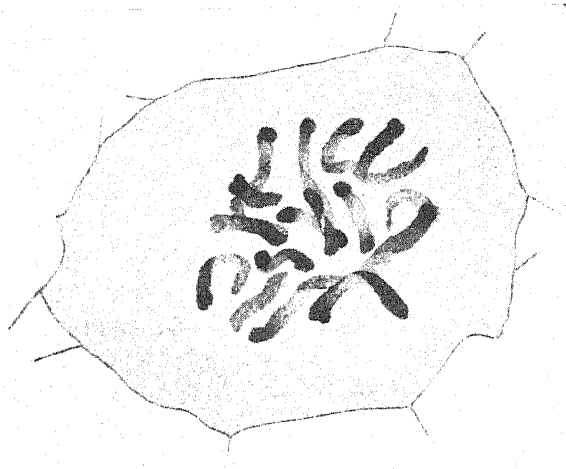


Fig. 1 Typical nuclear plate from root-tip of *Trautvetteria*

16 (see figure 1). These observations, therefore, support the most recent conclusions of Langlet, namely, that the diploid chromosome number of *Trautvetteria carolinensis* is 16.

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## Descriptions of tropical rusts<sup>1</sup>

GEORGE B. CUMMINS

WITH TWO TEXT FIGURES

In the following pages one new genus, four new species and two new combinations are described, together with notes regarding the relationship of some of the genera involved. The writer is indebted to John A. Stevenson of the Bureau of Plant Industry, United States Department of Agriculture, for furnishing the specimens upon which the descriptions of the new species are based and to Dr. O. A. Plunkett for the specimen of *Phakopsora jatrophicola*.

### *Lipocystis* gen. nov.

Pycnia subcuticularia, aparaphysata. Aecia subcuticularia, peridio destituta; aeciosporae solitarie in apice pedicelli natae, poris germinationis instructae. Uredia conformibus. Telia subcuticularia; teliosporae unicellulares, solitarie in apice pedicelli natae, inter se liberae vel interdum leniter conjunctae et capitula formantes, apice poro germinationis unico instructae; cystidia nulla.

*Lipocystis caesalpiniae* (Arth.) comb. nov. (*Ravenelia caesalpiniae* Arth., Bull. Torrey Club 31: 5. 1904; *Uromyces caesalpiniae* Arth., Mycologia 7: 183. 1915), a rust inhabiting *Mimosa ceratonia* L. in the West Indies, is the type of the genus and the only species known.

*Lipocystis* differs from *Ravenelia* and the various genera previously segregated from it by the absence of cysts. The genus is apparently closely related to *Ravenelia*. There are two features which indicate such a relationship. Firstly, the tendency to produce irregular, laterally united clusters of a few spores is reminiscent of the spore-heads in *Ravenelia*. Secondly, the spores have their origin from a cellular sheet, one to three cells in thickness, which is also true of certain of the subcuticular species of *Ravenelia*. This sheet appears to be a definite tissue underlying the entire sorus. The pedicels remain attached to the tissue and the tendency to form irregular clusters of united spores seems to be due more to this continued connection than to an actual adherence of the spores themselves.

Examination of the type of *Ravenelia caesalpiniae* proves that telia are present, although they were not described by Arthur when he published the species.

### *Dicheirinia guianensis* sp. nov. (fig. 1).

Pycniis amphigenis, subcuticularibus, conicis, maculis incrassatulis usque

<sup>1</sup> Contribution from the Botany Department, Purdue University Agricultural Experiment Station, Lafayette, Indiana.

5 mm. diam. occupantibus; paraphysibus nullis. Aeciis uredinoidis, gregariis, inter pycnia sparsis, plus minusve profunde immersis, 100–350  $\mu$  diam., castaneo-brunneis; paraphysibus copiosis ad marginem cingentibus, ramosis, septatis, cellulis terminalis capitatis, 16–30  $\mu$  latis, membranibus 1  $\mu$  cr., flavis vel ad apicem 5–12  $\mu$  et castaneo-brunneis; aeciosporis irregulariter triangularis, lateraliter 3-lobatis, 29–40 $\times$ 39–50  $\mu$ ; membranibus 1.5–2  $\mu$  cr., castaneo-brunneis, sparse et valde echinulatis, poris germ. 3, aequatorialibus. Soris uredio-

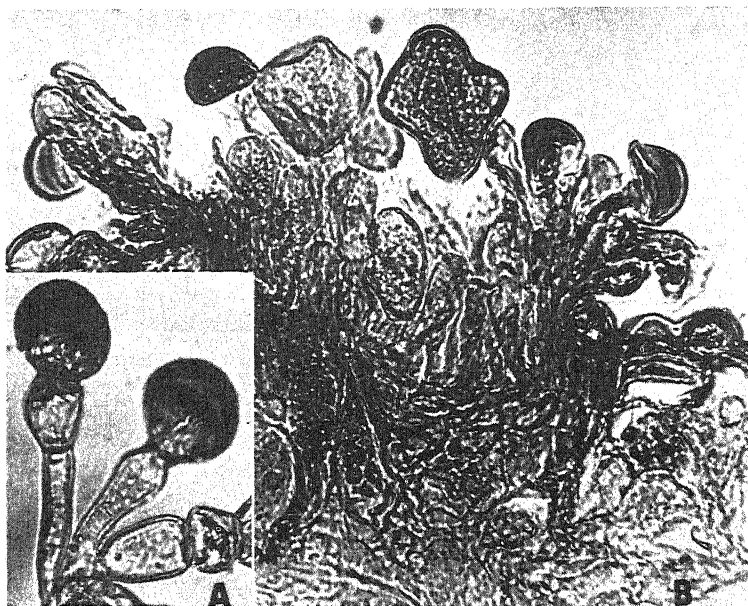


Fig. 1. A. *Dicheirinia guianensis*; a photograph of the spore-like paraphyses.  $\times 600$ . B. *Dicheirinia guianensis*; a photograph of a free-hand section of an uredium.  $\times 500$ . Note the peripheral paraphyses and the large lobate urediospores. The telia are similar in size and structure.

sporiferis (fig. 1, B) hypophyllis, aeciis conformibus sed sparsis et sine maculis. Teliis primariis inter aecia sparsis; teliis secundariis urediis conformibus; teliosporis irregulariter triangularis, ex 3 cellulis compositis, cellulis individuís triangularis, ellipsoideis vel oblongis, 17–26 $\times$ 25–40  $\mu$ ; membranibus 2–2.5  $\mu$  cr. vel ad apicem leniter incrassatis, castaneo-brunneis, ad apicem processibus tuberculatis 3–8  $\mu$  cr. praeditis, ad basim plus minusve levis; pedicellis flavis, pariete inferiore fragilis, unicellularis, pariete superiore ex 2 vel 3 cellulis compositis.

On leaves of *Lonchocarpus nicou* DC., Bonisiki Landing, Arawau River, N. W. District, British Guiana, July 7, 1934. W. A. Archer H-256. Host determined by E. P. Killip. Type specimens deposited in the Arthur

Herbarium, Purdue University and in the Mycological Collections of the Bureau of Plant Industry, United States Department of Agriculture.

*Dicheirinia guianensis* is an unique and interesting rust, possessed of morphologic features unusually distinctive. The pycnia offer no special features, being subcuticular, paraphysate and protected by the rupture cuticle of the host only.

The aeciospores and urediospores are alike in form and size. Apically the spores (fig. 1, B) are broadly rounded, basally they are rather abruptly narrowed to the hilum. Three prominent, lateral, equidistant lobes, located slightly above the equator, give an irregularly triangular shape to the spores. When a spore is viewed from the apex the appearance is that of an equilateral triangle, with the angles narrowly rounded. One pore is situated in each of the angles.

Branched paraphyses (fig. 1, A) are produced in abundance in the aecia, uredia and telia, their terminal portions so septate and modified as to closely simulate teliospores of a *Puccinia* or an *Uromyces*.

The pedicels of the teliospores are composed of a basal cell surmounted by two or three apical cells, the latter with vertical septa. Each of the apical cells may bear one cell of the teliospore or, when only two, one of them is attached to two cells of the teliospore. The teliospores are so similar in structure to those of *D. manaosensis* (P. Henn.) Cum. that the reader is referred to illustrations of the latter species published by the writer.<sup>2</sup>

In 1935 the writer (*l.c.*) pointed out that the teliospores of *D. superba* Jacks. and Holw. are similar in structure to the 2-celled teliospores of *Ravenelia simplex* Diet. *D. guianensis* furnishes additional evidence that *Dicheirinia* is closely related to *Ravenelia*. The aecia, aeciospores and urediospores and the branched septate, spore-like paraphyses find an almost exact counterpart in *R. bakeriana* Diet. (*Uredo margine incrassata* P. Henn.), which also parasitizes *Lonchocarpus*. The urediospores have the same shape, with the pores located in three lateral lobes, but those of *R. bakeriana* are slightly smaller. Aside from differences in teliospores the two species are very similar. It seems probable that *R. bakeriana* may have given rise, by a simplification of the teliospores already initiated within the species, to *D. guianensis* and it, in turn, to *D. manaosensis* and finally *D. archeri*, which is typical of the 2-celled species of *Dicheirinia*.

*Atelocauda incrustans* Arth. and Cum., also on *Lonchocarpus* might, with considerable justification, be considered as directly derived from *Dicheirinia* by continued simplification. Since the teliospores are reduced

<sup>2</sup> Mycologia 27: 151-159. 1935.

to single cells it would seem logical that the pedicels should also become unicellular structures.

*Dicheirinia archeri* sp. nov. (fig. 2).

Pycnia amphigenis, conicis, maculis incrassatulis usque 4 mm. diam. occupantibus; paraphysibus nullis. Aeciis et urediis nullis. Teliis amphigenis, inter pycnia sparsis, profunde immersis, 100–200  $\mu$  diam., castaneo-brunneis; paraphysibus copiosis ad marginem cingentibus, ramosis, septatis; cellulis terminalis clavatis vel capitatis, 8–20  $\mu$  latis; membranis hyalinis vel sub-brunneis, 1  $\mu$  cr. vel ad apicem 3–10  $\mu$ ; teliosporis plus minusve globosis, ex 2 cellulis compositis, cellulis individuis ellipsoideis vel oblongis, 19–28  $\times$  32–40  $\mu$ ; membranis 1–1.5  $\mu$  cr., castaneo-brunneis, ad apicem processibus tuberculatis 3–8  $\mu$  cr. coronatis, ad basim plus minusve levis; pedicellis hyalinis, pariete inferiore fragilis, unicellularis, pariete superiore ex 2 cellulis compositis.



Fig. 2. A. *Dicheirinia archeri*; photograph of a free-hand section of a pycnium.  $\times 550$ . B. *Dicheirinia archeri*; photograph of a teliospore.  $\times 550$ .

On *Lonchocarpus nicou* DC., Scotelweg, Surinam, November 2, 1934. W. A. Archer H-256. Host determined by E. P. Killip. Type specimens deposited in the Arthur Herbarium, Purdue University and in the Mycological Collections of the Bureau of Plant Industry, United States Department of Agriculture.

The teliospores of this microcyclic species correspond in structure to those of *D. binata* (Berk. & Curtis) Arth., the type of the genus, and to *D. superba* Jacks. & Holw. The species differs from *D. binata* in life cycle and teliospore sculpture and from *D. superba* in size. Aside from the differences in life cycle and number of cells in the teliospores *D. archeri* is similar to *D. guianensis*, both in the size and sculpturing of the teliospores and in the paraphyses. The terminal portions of the paraphyses are less differentiated than are those of *D. guianensis*, however.

When the writer (*l.c.*) reviewed the genus, it was with some trepidation

that the generic definition was expanded to include *D. manaosensis*. The discovery of *D. guianensis* and its obviously close relationship to *D. archeri* leaves no doubt that such species should be included in the genus.

*Uredo roupalae* sp. nov. = *Uredo maurise* Syd.

Uredii hypophyllis, subepidermalibus, maculis brunneis insidentibus, in greges orbiculares dense confertis; paraphysibus multis, ad marginem cingentibus, hyalinis, clavatis, medio septatis, pariete superiore solidis, 6–10  $\mu$  diam.; urediosporis obovoideis vel reniformis, 16–20 $\times$ 23–29  $\mu$ ; membranis 1–1.5  $\mu$  cr., cinnamomeo-brunneis, echinulatis, poris germ. 2, aequatorialibus.

On leaves of <sup>*Mauria glauca*</sup> ~~*Roupala tetraguensis*~~ Klotzsch, near San Jose, Costa Rica, 1928. *H. Schmidt* 2052. Type specimens deposited in the Arthur Herbarium, Purdue University and in the Mycological Collections of the Bureau of Plant Industry, United States Department of Agriculture.

The urediospores are radially asymmetric, being obovoid when the pores are seen in optical section but reniform with the pores in face view. The pores are located at the widest part of the spore. The paraphyses are, however, the characteristic feature of the species. A septum divides the paraphysis into a basal, thin-walled stipe and a somewhat irregular club-like head which is solid and highly refractive to light, giving it a silvery appearance.

*Puccinia molokaiensis* sp. nov.

Uredii hypophyllis, subepidermalibus, seriatim dispositis, brunneis; urediosporis obovoideis vel ellipsoideis, 21–28 $\times$ 28–40  $\mu$ ; membranis 2.5–3  $\mu$  cr., cinnamomeo-brunneis, aculeatis, poris germ. 2, aequatorialibus. Teliis conformibus; teliosporis oblongis, apice rotundatis, basi rotundatis vel attenuatis, medio non vel vix constrictis, 12–17 $\times$ 35–40  $\mu$ ; membranis levibus, 1.5  $\mu$  cr., ad apicem 4–6  $\mu$ , fulvis vel cinnamomeo-brunneis; pedicellis usque 40  $\mu$  longis.

On leaves of *Carex* sp., Molokai, Hawaiian Islands, April 12, 1928. *Degener and Wiebke* 2934. Type specimens deposited in the Arthur Herbarium, Purdue University, and in the Mycological Collections of the Bureau of Plant Industry, United States Department of Agriculture.

The species is characterized by large urediospores with thick, aculeate walls.

*Phakopsora jatrophicola* (Arth.) comb. nov. (*Uredo jatrophicola* Arth., *Mycologia* 7: 331. 1915).

Telia hypophyllous, subepidermal, indehiscent, surrounding the uredia, united into a crust 5–12 spores high; teliospores irregularly cuboid or oblong, 7–13 $\times$ 13–27  $\mu$ ; wall 1  $\mu$  thick or slightly thicker in the apical spores, chestnut-brown, the lower cells paler, sessile.



The description of telia is based upon a specimen collected on *Jatropha canescens* Muell.-Arg., in the Laguna Mountains east of Todos Santos, Lower California, Mexico, February 21, 1928 by Marcus E. Jones (24531). This rust, common in tropical North America, has not previously been reported from this region or on this host. The species also occurs in Brazil.

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## Notes on North American Xyridaceae

G. O. A. MALME

In reviewing the genus *Xyris* for North American Flora, the writer has found it necessary to propose the following new varieties and new combinations.

*Xyris Elliottii* Chapm. var. *stenotera* Malme, var. nov. Recedit a forma primaria foliis 12–16 cm. longis, 0.7–1 mm. latis, margine laevibus non incrassatis; pedunculis 35–45 mm. altis, circiter 1 mm. latis, laevibus, vagina circiter 10 cm. longa; spica pauciflora, 6–8 mm. longa, 3.5–4.5 mm. lata, bracteis floriferis circiter 5 mm. longis, 3–4 mm. latis, apice laceratis et saepe fusco-purpureis; sepalis lateralibus leviter exsertis vel inclusis, circiter 5 mm. longis; carina e medio apice lacerato-fimbriata.

Type, *G. V. Nash 443*, collected in Lake Co., Florida.

*Xyris Baldwiniana* Schultes, var. *tenuifolia* (Chapm.) Malme, comb. nov. *Xyris tenuifolia* Chapm. Fl. S. U. S. 502. 1860.

*Xyris torta* Smith, var. *occidentalis* Malme, var. nov. Recedit a forma primaria magnitudine; foliis 45–65 cm. longis, 2–3.5 mm. latis, laevibus; vagina opaca circiter 12 cm. longa, basi dilatata; pedunculis 60–75 cm. altis, circiter 1.5 mm. latis, laevibus, pedunculi vagina 12–15 cm. longa; spica multiflora ellipsoidea, 10–15 mm. longa, circiter 7 mm. lata, acuta vel subacuta, bracteis floriferis 5–6 mm. longis, 4–5 mm. latis, truncato-rotundatis et apice plerumque fimbriatis; sepalis lateralibus circiter 5 mm. longis et 0.75 mm. latis.

Type, *J. Reverchon 2763*, collected June 10, 1902, near Swan, Smith Co., Texas.

The variety is found in Texas and Arkansas, while forms somewhat intermediate between it and the usual form of the species are found in Georgia and Virginia.

*Xyris Smalliana* Nash, var. *Congdoni* (Small) Malme, comb. nov. *Xyris Congdoni* Small; Britton, Man. ed. 2. 1057. 1905.

*Xyris conocephala* Wright, var. *pallescent* (C. Mohr) Malme, comb. nov. *Xyris torta* var. *pallescent* C. Mohr. Contr. U. S. Nat. Herb. 6: 428. 1901. *Xyris pallescens* Small, Fl. SE. U. S. 234. 1903.

NATURHISTORISKA RIKSMUSEET  
STOCKHOLM, SWEDEN

# INDEX TO AMERICAN BOTANICAL LITERATURE 1933-1936

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material, the word America being used in the broadest sense.

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D. MAR.

Studies in the genus *Glonium* as represented  
in the Southeast<sup>1</sup>

M. L. LOHMAN<sup>2</sup>  
(WITH PLATES 1 AND 2)

LIBRA

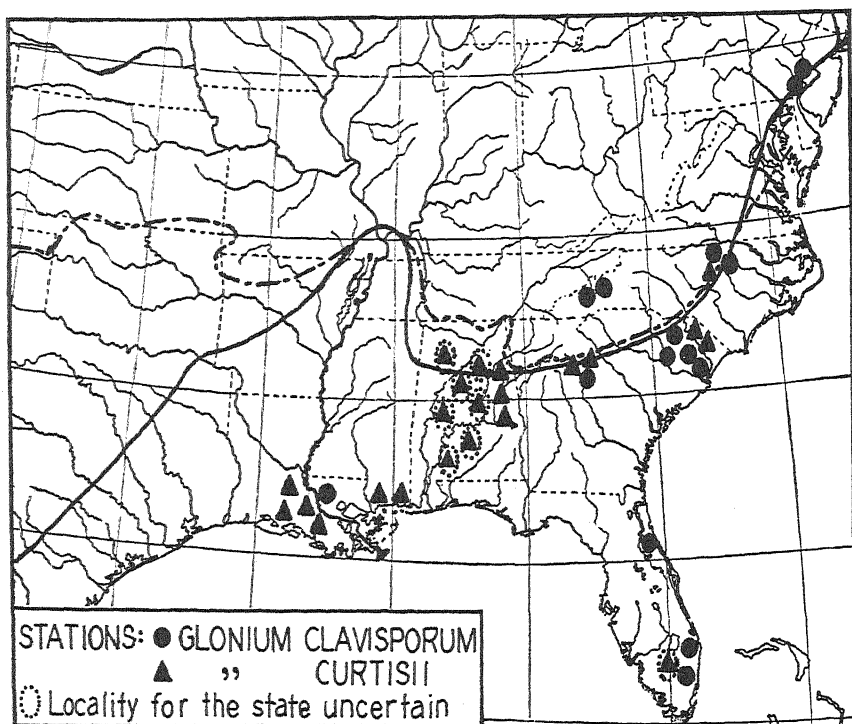
While in the region of northern hardwoods casual collections of the Hysteriaceae on broadleaved hosts are likely to be species of *Gloniopsis*, *Hysterium*, or *Hysterographium*, such collections in the southeastern states are likely to be species of *Glonium*, whether the substratum be the bark of logs or living trees, weathered wood, or recently fallen twigs. For the identification of hysteriaceous fungi found in this climatic zone Ellis and Everhart's North American Pyrenomycetes, in the main, and the compilations by Underwood and Earle (1897) and Earle (1901) have long been ready references.

When considered together the early treatments mentioned list or describe twelve species, six of them apparently limited in distribution to the area. Herein, the writer by exclusion of species or by synonymy of some of the names reduces the previously reported species to five, namely, *G. stellatum* Muhl. ex Fries, *G. abbreviatum* (Schw.) comb. nov. (*G. parvulum* (Ger.) Cooke), *G. lineare* (Fr.) De Not., *G. clavisporum* Seaver and *G. Curtisii* (Duby) comb. nov. (*Gloniella Curtisii* (Duby) Sacc.). *G. simulans* Ger., a species then only known northward, is added by extension of its range and *G. Finkii* (Petrak) comb. nov. (*Psiloglonium Finkii* Petrak), a Puerto Rican species, is included inasmuch as it may also be found to occur in the Coastal Plain. In addition, some results of cultural studies on *G. clavisporum*, *G. Curtisii* and *G. abbreviatum* are given since they are of interest in considering relationships and distribution. In the case of *G. clavisporum*, *Sporidesmium stygium* B. & C. is recorded as the conidial stage, the connection having been determined culturally. *G. velatum* E. & E., an excluded species (Lohman, 1934), is incorporated in the key for convenience. *G. graphicum* (Fr.) Duby and *G. varium* (Fr.) Sacc.,

<sup>1</sup> Contribution from the Laboratories of Cryptogamic Botany and the Farlow Herbarium, Harvard University, no. 144.

<sup>2</sup> The writer gladly acknowledges indebtedness to the National Research Council, the studies here reported having been completed as a part of an intensive study of life histories in the Hysteriaceae during the tenure of a fellowship in the Biological Sciences at Harvard University, 1931-33; to Professor William H. Weston, Jr., sponsor, and Dr. D. H. Linder, for laboratory facilities and instructive guidance; to the several mycologists who have kindly furnished living specimens for cultural investigations as noted in the treatment of species; and, for their generous cooperation in loaning specimens of historical interest or in giving information on type localities, to the officials in charge of the various herbaria noted in the citation of authentic specimens studied.

both of which were listed for the region by the early writers, are not included in view of the note by Bisby (1932) that the determinations were incorrect. In the case of *G. graphicum*, an European species, the writer has seen no American specimens of Hysteriaceae on either conifers or hardwoods referable to it. Of the six species discussed here for the Southeast, exclusive of *G. Finkii*, only *G. clavisporum* and *G. Curtisii* appear to be confined in their distribution to the Southern Forest region. These



Sketch map showing with reference to the general limits of the Coastal Plain (solid line) and the Lower Austral Life Zone (broken line) the known distribution of two species of *Glonium* in the United States.

species are found within the climatic province known as the Lower Austral Zone (*cf.* Bowman, 1911) and climatic elements such as mean low temperature, rainfall and humidity, rather than host relationship would seem to be the important factors limiting distribution. The close agreement between the known distributional ranges of these species and certain physiographic reference regions is shown in the accompanying map.

The genus *Glonium*, Muhlenberg, described by Fries, is used here as it is ordinarily recognized: that is, in the sense of De Notaris (1847).

Thus, except for conifer-inhabiting species with conchiform fructifications, all carbonaceous hysteriaceous fungi with hyaline or pale yellowish brown, oblong to fusiform 2-celled ascospores are admitted, framing the genus as a heterogeneous group of species as is evidenced by the wide and independent variation in habitat, structure and development of the fructifications and by the various types of paraphyses, ascospores and secondary spore stages among them. *G. Curtisii* with potentially muriform ascospores, for example, undoubtedly has its most closely allied species in other genera of the family. Some of the features of the fructifications that were emphasized in early descriptions are reactions to growth conditions and have little or no specific diagnostic value. Most important among them are obtuse versus acute ends, smooth or rugose as contrasted with striate appearance, degrees of superficiality and extent of blackening of the substratum. Within a species hysterothecia may develop superficially on bark or on transverse or radial surfaces of the wood, or they may develop between the elements of the wood on tangential surfaces. The markings on the fructifications depend upon age and periodicity in growth while the presence or absence of a black hyphal crust depends upon moisture conditions as well as on the character of the substratum. Since hysterothecia develop and mature in lines from their primordia the ends generally appear obtuse only in well matured ones. Similarly, degrees of prominence of the longitudinal groove are dependent upon maturity and amount of weathering of the fructifications. In the following key these features are employed wherever possible but only supplementary to microscopic features which are more useful and need not be discriminated against since as in most families of the Pyrenomycetes microscopic preparations are often necessary for generic determinations.

## ANALYTICAL KEY TO SPECIES

- A. Spores fusoid, elliptic-fusoid or clavate, averaging  $15-25\mu$  in length; hysterothecia superficial.
1. Hysterothecia in dichotomously branching lines which form loose or compact, irregular, fan-shaped or stellate composites on a black crust or brown subiculum; on decaying and decomposed wood. .... 1. *G. stellatum*
  2. Hysterothecia scattered or closely aggregated but if confluent, only in short simple lines; substratum sometimes blackened.
    - a. Up to 2 mm. in length; spores normally  $14-16 \times 4-5\mu$ ; on weathered wood. .... 2. *G. simulans*
    - b. Up to 3 mm. long; spores normally  $16-20 \times 5-7\mu$ ; on bark and wood and usually accompanied by dark masses of large globular conidia (*Sporidesmium stygium*) .... 3. *G. clavisporum*
    - c. Less than 1 mm. in length and sunken in the wood; spores averaging  $22-25 \times 3.5-4.5\mu$  and becoming 4-celled; on decaying wood and usually accompanied by a black crust and a dark web of elongate conidia (*Septonema multiplex*) .... *Lophiosphaera (Glonium) velata*



- B. Spores more or less ovoid or oblong (at least with the upper end rounded), averaging  $15\mu$  or less in length, the lower cell usually narrower and often tapering; hysterothecia superficial, or more or less imbedded and united laterally with the substratum.
1. Normally  $6-8 \times 2.5-3.5\mu$ ; hysterothecia averaging less than 1 mm. in length, usually densely crowded and blackening the substratum; on old weathered wood. .... 4. *G. abbreviatum*
  2. Normally  $12-15 \times 6-8\mu$ ; hysterothecia ordinarily more than 1 mm. in length, often confluent linearly, usually sunken; on firm weathered wood.
    - a. Asci cylindric clavate; about  $60\mu$  long. .... 5. *G. lineare*
    - b. Asci obovate, about  $40\mu$  long. .... 6. *G. Finkii*
- C. Spores cylindric, large, averaging  $65$  to  $70\mu$  in length; hysterothecia up to 1 mm. in length; generally on small twigs with bark intact. .... 7. *G. Curtisii*

1. *GLONIUM STELLATUM* Muhl. ex Fr. Sys. Myc. 2: 595. 1823.

Hysterothecia superficial, variable in length, following progressively on dichotomously branched and often radiating hyphal strands and forming irregular, labelliform, or stellate composites seated upon a conspicuous brown felt-like subiculum or a black crust, singly, merged or overlapping: asci cylindric,  $70-90(100) \times 8-10(12)\mu$ ; ascospores biseriate, elliptic fusiform, slightly curved, constricted at the septum,  $(18)20-24(28) \times (4)5-6(7)\mu$ , occasionally as much as 4-celled when arrested in germination.<sup>3</sup>

Pycnidia—*Sphaeronaema byssoideum* Lohman (1933)—common on the black crust,  $(150)170-200(215)\mu$  in width,  $(100)120-140(180)\mu$  in height exclusive of the beaks which reach  $200\mu$  in length; conidia hyaline, ovate to elliptic oblong,  $2 \times 1.5\mu$ , acrogenetic on simple conidiophores  $6-12 \times 1.5-2\mu$ .

This unmistakable fungus occurs on decaying wood, usually of broad-leaved species, throughout the southern states but is more common northward and perhaps most abundant in the Appalachians, especially on oak and chestnut. In rich woods it sometimes marks as a dark path in the litter, the length of some fallen and disintegrated veteran of the stand.

The exquisite patterns which the fungus forms in fruiting, or even the byssoid subiculum and black crust with pycnidia alone, are sufficient for the identification. In its ascospores the species must be grouped with *G. simulans* and *G. clavisporum*; in its pycnidial stage with *G. abbreviatum*. With respect to asci and spores the description given is an inclusive one taking into account material from Iowa, the Central States, New England, Louisiana and the Appalachian region. Measurements given by Ellis and Everhart (1892) and by Bisby (1932) for a Schweinitz specimen and the writer's for the preparation by von Höhnelt, marked "orig. Hildebrand Herbar." agree. Bisby (*op. cit.*) concludes that *Glonium accumulatum* Schw. is synonymous. Specimens that have the later fructifications piled upon the old, showing little symmetry, and that could be determined

<sup>3</sup> In the measurements recorded herein and in earlier publications on the Hysteriaceae two ranges, the normal and the extreme, are usually given, the latter when stated being in parentheses.

as *G. accumulatum* are not uncommon. They are morphological variations resulting from growth conditions and when fruiting is abundant typical specimens are usually found with them.

2. *GLONIUM SIMULANS* Gerard. Bull. Torrey Club 6: 78. 1876.

Hysterothecia superficial, scattered to closely aggregated, 0.5–2.0×0.3–0.4 mm., obtuse at the ends when mature, rugose punctate or finely longitudinally striate, usually seated upon a thin black crust; asci cylindric, (60)65–80(85)×(8)10–12(14) $\mu$ ; paraphyses branched above forming a pale yellowish, granular epithecium; ascospores elliptic-biconical, slightly curved, some becoming yellow-brown in old specimens, (10)14–16(18)×(4.5)5–6 $\mu$ , the upper cell usually broader than the lower at the septum.

Apparently a northern hardwood species but known to occur as far south as Tennessee; on wood. No secondary spore stages have been observed accompanying the hysterothecia and cultures have produced only sterile mycelia (Lohman, 1933). The species appears to be more closely related to *G. clavisporum* than to *G. abbreviatum* and *G. lineare* with which it has often been confused. As observed with a hand magnifier, the hymenium when dry is whitish to tan while in *G. clavisporum* it is pale to greenish yellow. Moreover, the hysterothecial walls are thinner and therefore more fragile and on the average the hysterothecia, asci and spores are smaller. *G. abbreviatum* has ascospores of about the same shape but only half as large. *G. lineare*, which differs strikingly in the structure of the fructification, has an oblong to ovoid spore,—scarcely twice as long as broad.

3. *GLONIUM CLAVISPORUM* Seaver. Mycologia 17: 4. 1925. Figs. 5–9; 13–15.

Hysterothecia superficial, prominent, straight or flexuous, rounded above and with obtuse ends, smooth or longitudinally striate, up to 2.2 mm. in length and 0.4 mm. in width; asci cylindric, 90–110×8–10(12) $\mu$ ; paraphyses branched above, oily granular, pale to greenish yellow in mass; ascospores elliptic to clavate-fusoid, slightly curved, constricted at the septum, uniseriate but overlapping, (15)16–18(20)×5–6 $\mu$ .

Scattered clusters of large dark conidia (*Sporidesmium stygium* B. & C.) associated.—Diagnosis based on the type specimen (Wood: Greytown, Nicaragua, 1896; C. L. Smith) at the New York Botanical Garden.<sup>4</sup>

While considerable variation has been noted in the size of the hysterothecia on different substrata, the ascospores have been found uniform in size and shape. In a collection on undetermined wood from Florida (Thaxter) the fruits are up to 3.5 mm. in length. In general, when on tangential surfaces of wood they are more elongate, often confluent linearly,

<sup>4</sup> In his original description Dr. Seaver indicated three collections (Puerto Rico, St. Croix, and Nicaragua) without designating a type specimen. Here, at his request, the earliest of the three is so named.

and usually straight, while when seated upon bark they are variable in length, irregularly scattered, and the longer ones often flexuous. They may be smooth or striate, scattered or densely crowded, with or without a black crust or the dark brown conidial masses. The asci measure  $(75)90-110(120) \times 8-10(12)\mu$ ; ascospores  $15-20(22) \times (4.5)5-6(7)\mu$ ; dark brown to black, single or clustered conidia  $(65-90)120-220(300) \times (30)50-90$ , averaging  $140-190 \times 60-85\mu$ .

Considering the hysterothecial stage alone the species is known on bark of logs and living trees and on firm weathered wood—*Vitis*, *Liquidambar*, *Sassafras*, *Platanus*, *Quercus* and undetermined deciduous species—from North Carolina to Florida, and from Louisiana. The conidial stage is known for these hosts, with the same distribution; also on bark of *Acer* from southeastern Pennsylvania (Michener) and on undetermined wood from the same locality (Schweinitz). Southward the species is distinct; northward it can easily be confused with the preceding species which is closely allied but has smaller ascospores and no known conidial stage. The *Sporidesmium* stage in habit and gross features cannot be distinguished from *S. epicoccoides* B. & C. but microscopically the conidia are small-celled parenchymatic and opaque while in *S. epicoccoides* they are prosenchymatic and translucent. They are somewhat smaller in the latter, measuring  $(92)120-142(180) \times (46)50-60(67)\mu$ .

*Sporidesmium stygium* B. & C., "*Monilia memorabilis*, herb. Schw.," "*Glonium simulans* f. *macrospora*, herb. Ellis," and *Glonium Ravenelii* Cooke & Phil. are synonyms. Authentic material (Ravenel Fung. Am. 763, in the Farlow Herbarium)<sup>5</sup> was found to contain only a few apparently immature or abortive asci and spores, as Bisby (1932) has noted for other distributions of this collection, and no conidia. Undoubtedly the sterile fruits of the collection are this species but with salient diagnostic features lacking in the type specimen the name perhaps should be discarded.<sup>6</sup>

<sup>5</sup> On *Platanus*, Seaboard, S. C. Ravenel's distribution of *Sporidesmium stygium* B. & C. on bark of *Platanus* (Fung. Car. 88) shows the hysterothecial stage with mature spores.

<sup>6</sup> Specimens examined, authentic or otherwise important:

*Glonium clavispurum* Seaver ("*Gl. simulans* f. *macrospora*, herb. Ellis"); Greytown, Nicaragua, 1896, C. L. Smith; type (New York Botanical Garden). *Glonium Ravenelii* Cke. & Phil.; Ravenel Fung. Am. 763; *Co-type* (FH, i.e., Farlow Herbarium, Harvard University). *Sporidesmium stygium* B. & C.: Curtis 3972 (Michener 1243), Maple log, (N. Garden, Chester Co.) Penna., 1852, *co-type* (FH); Curtis 2516 and 2338, *Coccularia Querc. lign. carios.*, 1849, Society Hill, S. C." (FH); Curtis . . . , "*Coccularia cort. Platani*, Santee Canal, S. C., Ravenel (1532)," accompanied by perfect stage (FH); Curtis . . . , "*Monilia memorabili*, Beth., herb. Schw." (FH); Ravenel, Fung. Car. 88, accompanied by perfect stage (FH). *Sporidesmium epicoccoides* B. & C.: Curtis 6322, "trunc. Viv. Platani, R. Island, Bennett (144)," *co-type* (FH).

Specific unity for *G. clavisporum* and the *Sporidesmium* was determined culturally. Well-formed conidia averaging  $120-190 \times 50-65\mu$ , successive developmental stages of which are illustrated (fig. 8), were obtained in single ascospore cultures made from Georgia and North Carolina collections.<sup>7</sup> Seemingly, certain definite conditions of humidity and temperature must be provided to obtain an abundance of normal conidia. Plate cultures on malt extract agar, encircled with rubber bands to prevent rapid drying, were kept for six months at approximately 10, 15, and 20 to 22°C. with light-exposed and light protected sets at the highest temperature. Examination at the end of the second month revealed a few immature conidia only in plates which had been held in the dark at 20° C. Examination of this series, and a second set of plates protected from light, at the close of the sixth month again showed sporulation only in cultures grown at 20°, with conidia somewhat more abundant but much more variable in the plates which were regularly exposed to diffused light. However, plates with the greatest amount of water of condensation showed the greatest variation in shape and size of conidia; with simple and multiple "broom" formations, chains of conidia (*Sirodesmium*), and conidia normal in shape and size but with apical outgrowths. Undoubtedly all of these variations occur in the field. Chains of conidia, simple or branched, are not uncommon in collected material.

These studies perhaps indicate that temperature is the critical factor in conidial production. The results are all the more interesting in view of the probable northern limit of distribution of the species as illustrated on page 58. Average radial growths of colonies for the series described are as follows: At the close of two months; at 10°—scant aerial growth on inoculum but no radial growth; at 15°—15 mm.; at 20 to 22°—23 mm. Average radial growths at two months of colonies in the sucrose-oatmeal agar medium (Lohman, 1933, p. 237) are: at 10°—scant aerial growth on inoculum but no radial growth; at 18 to 22°—28 mm. Mycelial development relative to temperature is, in this species, similar to that of *Ostreion americanum*, *Glonium Curtisii* and *Lophiosphaera velata*, all of which likewise appear to be limited to the Southern Forest region, rather than to the temperature relations of species of *Glonium* common to both temperate and austral zones (*op. cit.*, p. 244). On the sucrose-oatmeal agar medium the colonies in this species are dark greenish slate and produce a slight yellowish green discoloration of the medium, while in *G. simulans* they are light gray and produce a strikingly purplish discoloration.

<sup>7</sup> On *Vitis*: Princeton, Ga., February 1932; J. H. Miller. On *Liquidambar*, bark: Chapel Hill, N. C., November 1932; J. N. Couch. Respectively, numbers 466 and 503 in the writer's herbarium. Duplicates of these and similar collections mentioned herein by number have been deposited in the Farlow Herbarium.

4. *Glonium abbreviatum* (Schw.) comb. nov. (*Hysterium abbreviatum*, Schweinitz, Syn. Fung. Am. Bor., p. 245. 1832).

Hysterothecia short oblong, up to 0.5 mm. in length, smooth with obtuse ends, erumpent from between the fibers of the wood in more or less parallel series, tending to darken the substratum; paraphyses filiform, simple; asci short-cylindric,  $40-50 \times 4-5\mu$ ; ascospores oblong or ovoid with the lower cell somewhat the narrower, obliquely uniseriate, constricted at the septum,  $6.5-8 \times 2.5-3\mu$ .—Diagnosis based on type specimen from herbarium of Schweinitz in Curtis collections at Farlow Herbarium, labelled presumably by Curtis, "*Hysterium abbreviatum* Schw. in lign. *Rhododendri*."

Pycnidia—*Sphaeronaema parvulum* Lohman (1933)—superficial, single or clustered,  $150-200\mu$  in diameter,  $225-300\mu$  in height including the beak; conidia hyaline, ovate to inequilateral or elliptic-oblong,  $2 \times 1.5\mu$ , acrogenetic on simple conidiophores,  $6-9 \times 1.5-2\mu$ . The pycnidia are rarely found accompanying the hysterothecia but have been obtained in ascospore isolations of the species from specimens on *Tilia* and *Ulmus* from Michigan, *Acer* from Massachusetts, *Liriodendron* from North Carolina, and undetermined wood from Louisiana.

This species, which has been illustrated in an earlier publication (Lohman, 1931) under the name of *Glonium parvulum*, is widely distributed in hardwood forest areas of North America, occurring on firm weathered wood of various species. It is common throughout the southeastern region, apparently being most abundant on *Quercus*, *Liriodendron* and *Magnolia* in the Southern Appalachians. The short hysterothecia and small spores are distinctive features; whereas the pycnidial stage relates it closely to *G. stellatum*. In regard to other names that have been applied to American specimens of this species, there is good evidence that *Hysterium parvulum* Gerard (1874; *cfr.* Bisby, 1932) and *H. medium* Cooke are synonyms.

In general the hysterothecia are larger than in the Schweinitz specimen; occasionally, up to 1.5 mm. in length as in Ravenel's Fung. N. Am. 293 (at the Kew Herbarium) which is the type (on *Berchemia*: Texas) of *Hysterium medium* Cooke. However, they average less than 1 mm. in length; may be smooth or faintly striate; crowded irregularly on transverse surfaces, where they are usually seated on a black crust; or aggregated in more or less parallel series on tangential surfaces where they are often sufficiently dense so as to blacken the wood. In general the asci measure  $40-55(60) \times 4-5(6)\mu$  and the ascospores, which may be obliquely uniseriate to sub-biseriate, measure  $6-8 \times (2)2.5-3(3.5)\mu$ . As to the synonymy of Cooke's name a cultural study of material from Louisiana<sup>8</sup> in which the

<sup>8</sup> On weathered wood, Baton Rouge, La., December 1931. Collection by A. H. Smith; number 458 in the writer's herbarium.

hysterothecia were equally as large as in the type specimen of *Hysterium medium*, supports the present contention which the writer shares with Bisby (1932).

Single ascospore cultures from the Louisiana specimens produced pinkish to vinaceous mycelia with a purplish discoloration of the medium and a pycnidial stage of the *Sphaeronaema* type just as had been observed in the cultural study of specimens from Michigan (Lohman, 1931, 1933), Massachusetts and North Carolina in which the hysterothecia were smaller. In their growth rates relative to temperature (10 and 22°) all cultures were identical, possibly indicating for the southern specimens studied no special adaption to the warmer climate.

Although this *Glonium* has become fairly well established in the literature on the basis of the epithet *Hysterium parvulum* assigned to it by Gerard (1874), with careful consideration its specific name is altered here on the conviction that such action is implied in the systematic details presented and by the fact that proposals of *nomina specifica conservanda* are now generally meeting with disfavor.

5. GLONIUM LINEARE (Fr.) De Not. Giorn. Bot. Ital. 2 (2): 27. 1847.

Hysterothecia usually in parallel series on tangential surfaces of firm wood and accompanied by a thin black crust, variably elongated, averaging about 1.5 mm. but often confluent linearly, at first narrow with a fine longitudinal fissure, later up to 0.4 mm. broad with the black epithecium more or less exposed, developed within the wood and not easily freed, with the flat stromatic top scarcely above the surface at maturity and the lateral walls poorly developed and light colored below; paraphyses branched and united above into a bluish brown granular mass; asci cylindric clavate, when not extended measuring (55)60–75(90)  $\times$  (10)12–14 $\mu$ ; ascospores obliquely uniseriate or sub-biseriate, oblong or ovoid, the lower cell often narrower, constricted at the septum, (10)12–15  $\times$  (5)6–8 $\mu$ .

Pycnidia preceding and bordering the hysterothecial aggregates, arising within the wood and then erumpent by their short papillae, (150)200 to 300 $\mu$  in diameter; conidia hyaline, 1-celled, elliptic-oblong, 2.5–3  $\times$  1.5–2 $\mu$ , acrogenetic on slender conidiophores accompanied by longer septate sterile filaments. This is of the *Plenodomus* type (Lohman, 1933). From European collections of the species it has been described by Hilitzer (1929) as *Hysteropycnis globularis*.

This species, easily overlooked and seldom reported, is probably generally distributed in the southeastern region on firm wood of various hardwood species, but is apparently less abundant here than northward. The long flat fructifications, dark epithecium and broad ascospores are distinctive features. *Hysterium lineare* Fr., among a number of early

names that were applied to European collections, and *H. Kalmiae* Schw. are important synonyms.<sup>9</sup> In early literature on American fungi various species of the Hysteriaceae have been referred erroneously to *H. lineare*.

6. *Glonium Finkii* (Petrak) comb. nov. (*Psiloglonium Finkii*, Petrak, *Anal. Myc.* 21: 308. 1923).

Hysterothecia deep seated on tangential surface of the wood and not easily separable, 1 to 2.5 mm. long, flattened, stromatic, with poorly developed lateral walls hyaline below; paraphyses delicate, branched above, forming a dark granular epithecium; asci broad saccate, tapering to a short stalk, thick walled at the apex; ascospores irregularly grouped in upper part of ascus, elliptic oblong, the upper cell broad with rounded end and the lower narrower, (12)13–15 $\mu$  long, 6–7 $\mu$  wide in the upper cell, (3.5)4–5 in the lower.—Diagnosis based on co-type (Fink 1446 in Herbarium of the New York Botanical Garden); on weathered wood from dry hill top, Yauco, Puerto Rico.

This species is known only from Puerto Rico but is included here inasmuch as it is likely to be found in this region. Although resembling *G. lineare* both superficially and in the morphological development of the hysterothecia, it is distinct with respect to asci, paraphyses and epithecium. In fact the grouping of the ascospores in short broad thick-walled asci suggests a rather distant, yet subgeneric, relationship with that species. A pycnidial stage was not found in the collection examined and a cultural study of the species has not been possible for lack of living specimens.

7. *Glonium Curtisii* (Duby) comb. nov. (*Hysterium Curtisii*, Duby, *Mém. Soc. Phys. et Hist. Nat. Gen.* 16: 30; t. 1, fig. 1. 1861). Fig. 1–4; 10–12.

Hysterothecia scattered, breaking through the bark or periderm but appearing superficial at maturity, narrow to broad elliptic, subconchiform, 0.5–0.7(1)×0.5 mm., black, smooth or finely striate; asci with walls thickened apically, broad cylindric, 155–180×30–35 $\mu$ , with short or inconspicuous stalk and fine filiform granular paraphyses branched above in an oily-granular matrix, the mass sordid white to pale citron; ascospores cylindric with rounded ends, slightly curved, hyaline to pale greenish or yellow-brown, biseriolate, (59)62–68(76)×13–15 $\mu$ , constricted at the septum with the lower cell about one third the length of the spore and the end walls, especially the upper, thickened with age in such a manner that the endoplasts appear cup-shaped

<sup>9</sup> Authentic materials examined: *Hysterium lineare* Fries, *Scler. Suec.* 90 (FH), with hysterothecia and ascospores as described above (cfr. Rehm, 1886, and Bisby, 1932).

*Hysterium Kalmiae* Schw., "in lign. Kalmiae herb. Schw. (a)," co-type (FH), with hysterothecia and ascospores as described above. Billings (1871), Ellis and Everhart (1892) and Bisby (1932), having found other Schweinitz specimens under this name to be undeterminable, list this as a doubtful species.

at the ends and the cells pseudoseptate.—Diagnosis based on the type specimen ("*Hysterium flexuosum* Schwein. in Vite, S. Carolina, M. A. Curtis") in the Duby collections at Strasbourg.

This is a common and extraordinary species which because of its peculiarities has led to considerable confusion in the determinations and writings by early mycologists. It is known to occur in the Coastal Plain from North Carolina to Florida and Louisiana (see map, page 58) on

TABLE 1  
*Measurements of hysterothecia and ascospores in important collections of Glonium Curtisii*

COLLECTION	HYSTERTHECIA (mm.)	ASCOSPORES ( $\mu$ )
<i>Hysterium Curtisii</i> Duby on <i>Vitis</i> , S. C. Type	0.5–0.7(1)×0.5	(59)62–68(76)×13–15
ditto	.....	40×11*
ditto	1–1.5×1	45–60×10–12**
<i>Hysterium chlorinum</i> B. & C. on twigs of <i>Quercus</i> , Ala. Type	.....	–72 long***
ditto Co-type	0.5–1×0.3–0.5	.....
<i>Hysterium Cyrillae</i> B. & C. on twigs of <i>Cyrilla</i> , S. C. Type	0.5–1×0.3–0.7	54–82×13–17***
ditto Co-type	ditto	.....
<i>Glonium macrosporium</i> Tracy & Earle; twigs of <i>Persea</i> , Miss. Type	0.5–0.7×0.4	(59)64–75×13–15
<i>Glonium gigasporum</i> E. & E. on <i>Vitis</i> , La. (Fl. Ludov. 1197). Co-type	0.5–1.2×0.5	67–74(78)×(12.5)14–15

\* As given by Thümen, 1878; \*\* Rehm, 1886; \*\*\* Bisby, 1932.

small twigs and stems of various broadleaved species, especially *Berchemia*, *Castanea prunella*, *Cyrilla*, *Persea*, *Prunus*, *Quercus aquatica* and *nigra*, *Rubus*, *Sabal*, *Smilax* and *Vitis*. No hyphomycetous or pycnidial stages have been observed accompanying the hysterothecia and ascospore cultures of the species have produced only sterile mycelia.<sup>10</sup>

*Hysterium Cyrillae* B. & C., *H. chlorinum* B. & C., *Gloniella Curtisii* Sacc., *Glonium macrosporium* Tracy & Earle, "*Glonium gigasporum* E. & E. in herb. Ellis" and *Hysterothecium Curtisii* Duby (Earle, 1901) are important synonyms.<sup>11</sup>

<sup>10</sup> Isolations from specimens on dead twigs of *Quercus nigra* collected by J. H. Miller, Princeton, Ga., February 23, 1932; No. 464 in the writer's herbarium.

<sup>11</sup> Specimens examined, authentic or otherwise important: *Hysterium Curtisii* Duby: "*Hysterium flexuosum* Schwein. in Vite, S. Carolina, M. A. Curtis," type—Herb. Inst. Bot., Strasbourg. *Hysterium chlorinum* B. & C.: Curtis 4637 (Beaumont 174.5), on twigs of *Quercus aquatica*, Ala., co-type (FH); Curtis . . . (Beaumont 464), stems of *Rubus*, 1854, Ala. (FH); Curtis 4573 (Peters 558), on undetermined twigs, 1854, Ala. (FH); Curtis . . . (Peters 689), on twigs of *Berchemia*, 1854, Ala. (FH). *Hysterium*



The hysterothecia sometimes are a little longer than in the type specimens but even then average about 0.7 mm.; they may be smooth, or rugose with several prominent lines paralleling the longitudinal groove (as in *Glonium gigasporum*); externally black and shining or with a conspicuous green powdery coat (as in *G. gigasporum* and *Hysterium chlorinum*) apparently resulting from expelled spore contents and granules from the epithecium which adhere to the fructifications and surrounding substratum. The asci are variable in size, sometimes measuring as much as  $200-220 \times 40\mu$  (as in *G. macrosporium*) or even larger when the spores begin to germinate within the ascus. Greatest diversity in appearance of the ascospores is in the emargination of the endoplast which accompanies the progressive lamellate thickening of the end walls (fig. 1 and 2). This feature is seen best in preparations in which osmic acid, or cytoplasmic stains in a solution of lactophenol have been employed. In temporary preparations made on routine examination of specimens, the plug in the upper half of a mature spore generally swells appreciably in a water mount and considerably if a weak solution of sodium or potassium hydroxide is used. With sufficient swelling the wall of the spore is broken at the junction of the plug and endoplast and the spore appears 3-celled as it has sometimes been described. If a weak base is used as a swelling agent, after some time many spores show distended plugs (fig. 4) which occasionally are five to ten times the length of the normal spore.

Variation in size of spores in individual specimens, as may be seen in table 1, is not extreme when compared with that feature in any other species such as *G. abbreviatum*. For the species the ascospores measure  $(55) 62-74(78) \times 12-16\mu$ . It is surprising that with the number of descriptions that have appeared, not one has correctly depicted this ascospore. That by Rehm (1886), based on the type specimen, is best and is adequate with the exception that he referred to the lower cell of the spore as the upper and that his spore measurements fall below the average. As to illustrations, that by Billings (1871, fig. i) shows a better interpretation than those by Duby and Thümen. The study of stained spores from various collections and the observation of germinating spores clearly indicate that they are 1-septate as figured by Billings and later described by Berkeley and Curtis and by Tracy and Earle.

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Cyrrillae B. & C.: Curtis 2747, dead twigs of *Cyrrilla*, 1849, S. C., type—Kew Herbarium; co-type (FH). *Gloniella Curtisii* (Duby) Sacc.: Ellis, N. Am. Fung. 1221, on *Sabal serrulata*, Fla.—Kew Herbarium. *Glonium gigasporum* E. & E. in herb. Ellis: Fl. Ludov. 1197, on *Vitis*, 1889, La.; 2298, on *Smilax*, 1890, La.; 2299, on *Berchemia*, 1890, La.—all collections by Langlois (FH). *Glonium macrosporium* Tracy & Earle: On twigs of *Persea*, Earle, 1895, Miss., type (FH).

Unlike small-spored species of *Glonium* the ascospores of *G. Curtisii*, germinating upon nutrient agar, show a number of tubes none of which are apical (fig. 3). They are scattered over the spore but, if it is not broken at the septum, tend to be concentrated in two whorls, one at the septum and one at the junction of the endoplast and plug in the upper cell. With the swelling of the endoplasmic "sporules" and the plugs, many spores break at the septum. Then either the sporules are extruded or many germ tubes emerge from the break. The numerous sporules and germ tubes indicate a merenchymatic condition of the endoplasm similar to that which occurs in certain species of *Gloniopsis* and *Hysterographium*. However, the unique plugs with their apparent function of expelling the endoplasm indicate an unusual species with no close relatives in North America.

In culture on maltose-malt extract and sucrose-oatmeal media this species grows very slowly at moderately low temperatures and has a relatively low growth rate even at room temperature. On the latter medium the radial growths of mycelial mats at the end of two months averaged 3 mm. for cultures that had been held at 8 to 10° and 14 mm. for cultures at 18 to 20°. The mycelial mats produced were erumpent, thick and more or less stromatic, light greenish slate at first as in *Hysterographium* [*vulvatum*] *flexuosum* (Schw.) Rehm and *H. kansense* E. & E. (Lohman, 1933) but becoming during the second month somewhat lighter in the color of the superficial hyphae with copious dark brown viscous droplets.

#### SUMMARY

Further cultural life-history studies in the genus *Glonium*, based on specimens collected in the warmer southeastern portion of the United States, have shown the desirability of simplifying considerably the taxonomy of American species and have furnished another connection between the Hysteriaceae and the form genus *Sporidesmium*. Results of the studies are incorporated in a systematic account of the species known to occur in the Southeast on bark or wood of broadleaved hosts.

Seven species, four of which are found elsewhere in the United States, are recognized and described—with diagnoses based on authentic specimens so far as possible and the variability of such species considered separately. An analytical key to species is provided showing some possible subgeneric relationships otherwise not discussed independently in the text.

Two species, *Glonium Curtisii* (Duby) Lohman and *G. clavisporum* Seaver, are particularly interesting for they appear to be limited in their distribution in the United States to the Southeastern Forest region, pos-

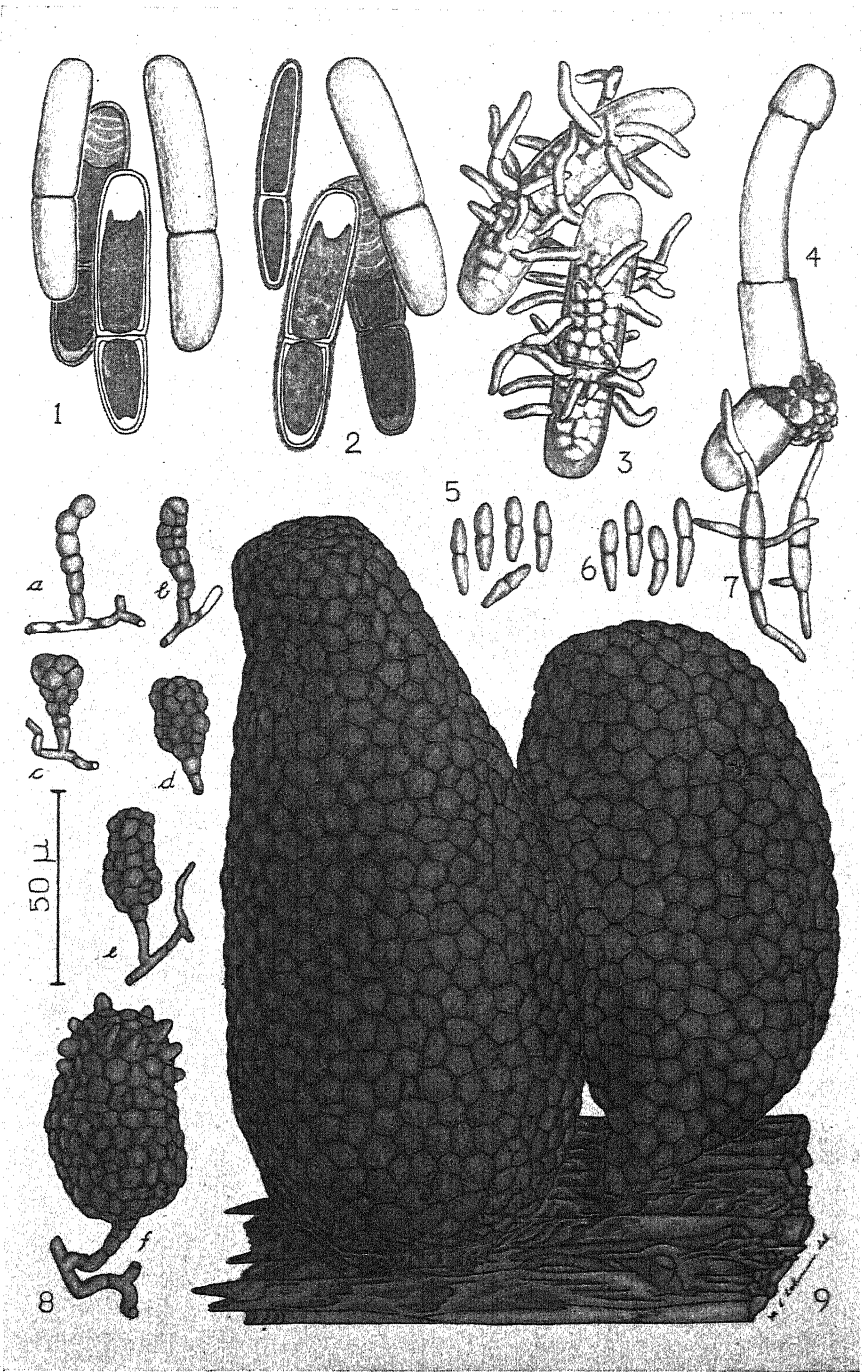
sibly by temperature and moisture rather than host relationship for in culture on favorable nutrient media their colony growth is greatly inhibited by moderately low temperatures (8 to 10° C.) and in the latter species while cultures produced conidia in abundance at 20 to 22° they produced only sterile mycelia at 10 and 15°.

The conidial stage discovered in the case of *G. clavisporum* is *Sporidesmium stygium* B. & C., a Hyphomycete especially interesting for its large sclerotoid conidia. Seemingly, this is the first hyphomycetous stage known for the genus *Glonium*.

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LOHMAN: GLONIUM

## Explanation of plates

Illustrating the ascospores and hysterothecia of *Glonium clavisporum* Seaver and *G. Curtisii* (Duby) and the conidial stage (*Sporidesmium stygium* B. and C.) of the former species. The drawings were outlined to the same scale with the aid of the camera lucida and as reproduced represent an approximate magnification of  $530\times$ . The photographs illustrate the hysterothecia at a magnification of  $30\times$  and the conidia (fig. 15) at  $60\times$ .

## Plate 1

Figures 1-4. *Glonium Curtisii* (Duby)

Fig. 1. Ascospores of the *type* specimen (*Hysterium Curtisii* Duby, on *Vitis*; South Carolina) with two stained spores shown in section view to illustrate the condition of the endoplast and the apical plug at maturity—left section view, osmic acid stain; right, cotton blue in lactophenol.

Fig. 2. Ascospores of the specimen cultured (464, on *Quercus nigra*; Georgia) with three stained spores shown in section view—left section views, one immature and one mature spore as observed after staining with cotton blue in lactophenol; right, osmic acid stain.

Fig. 3. Germination of spores upon nutrient agar medium.

Fig. 4. Extension of the plug and rupture of the spore following treatment with weak potassium hydroxide.

Figures 5-9. *Glonium clavisporum* Seaver

Fig. 5. Ascospores of the *type* specimen (on old wood; Nicaragua).

Fig. 6. Ascospores of one of the specimens cultured (466, on *Vitis*; Georgia).

Fig. 7. Typical germination of spores on nutrient agar medium.

Figs. 8 and 9. The *Sporidesmium* conidial stage; fig. 8 illustrating early stages in development in single ascospore cultures on nutrient agar medium and fig. 9, mature conidia in collection 466—the same in all respects as mature conidia obtained in culture. The conidia are found commonly in association with the perfect stage on both wood and bark.

## Plate 2

Figures 10-12. *Glonium Curtisii* (Duby)

Fig. 10. Surface and lateral views of hysterothecia in the collection from which isolations were made (i.e., 464, on *Vitis*; Georgia).

Fig. 11. Hysterothecia in the *type* specimen (on *Vitis*; S. Car.) herb. Duby.

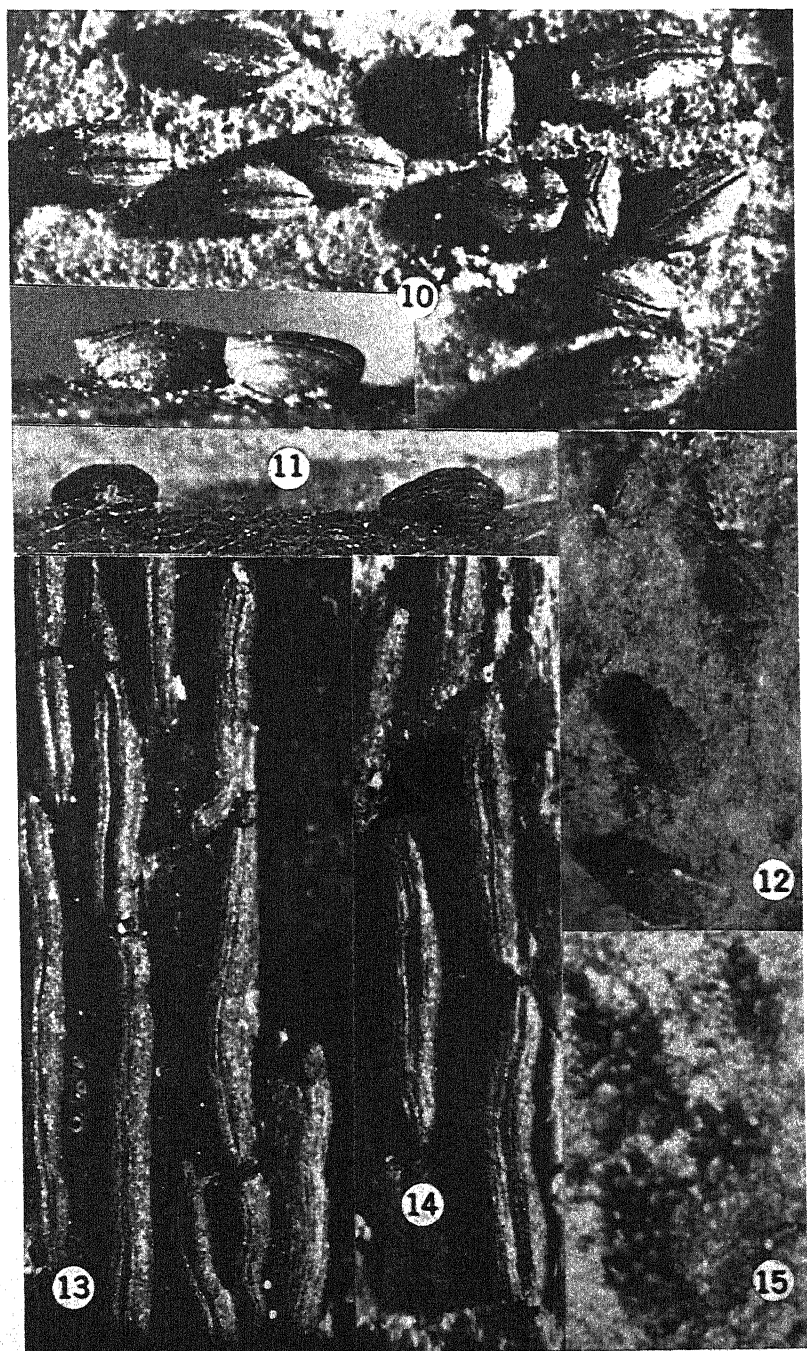
Fig. 12. Hysterothecia in the *type* collection of *Glonium macrosporium* Tracy and Earle (on *Persea*; Mississippi).

Figures 13-15. *Glonium clavisporum* Seaver

Fig. 13. Hysterothecia in one of the collections from which isolations were made (i.e., 466, on *Quercus nigra*; Georgia).

Fig. 14. Hysterothecia in the *type* collection (on old wood; Nicaragua), herbarium of the New York Botanical Garden.

Fig. 15. *Sporidesmium* conidia accompanying the perfect stage in one of the collections cultured (i.e., 503, on bark of *Liquidambar*; North Carolina).



LOHMAN: GLONIUM



## The life history of a new species of *Mesotaenium*<sup>1</sup>

CLARENCE E. TAFT

### *Mesotaenium aplanosporum* sp. nov.

Cellulis oblongis, cylindracis, apicis orbiculatibus, in orbem flexus; longitudinibus  $1\frac{1}{2}$ – $2\frac{1}{2}$  frequenter majorim diametrim, curvatis leviter; coloro corporo auxio orbox. Cellulis in gelatis matricis inditis.

Zygosporis globosis vel ovatis; globosis abnormis saepe, extero muro papillatio densiter et abnormiter; rubeis fuscis coloribus.

Aplanosporis isdem formis quam vegetativis cellulis, papillatis; papillis postulatis in transversis ordinibus circumque semenibus, rubeis fuscis coloribus.

Cellulis vegetativis  $13$ – $17\mu$  latis,  $18$ – $35\mu$  longioribus; Zygosporis  $20$ – $23\mu$  latis,  $20$ – $27\mu$  longioribus; aplanosporis  $11$ – $14\mu$  latis,  $28$ – $34\mu$  longioribus.

Cells oblong-cylindrical, apices rounded, length  $1\frac{1}{2}$ – $2\frac{1}{2}$  times the diameter, slightly curved; chloroplast an axial plate. Cells embedded in a gelatinous matrix.

Zygospore globose to ovoid-globose, often irregular, outer wall densely and irregularly papillate, red-brown in color.

Aplanospores the same shape as the vegetative cell, papillate; papillae arranged in transverse rows about the spore. Color red-brown.

Veg. cell  $13$ – $17\mu \times 18$ – $35\mu$ ; zygospore  $20$ – $23\mu \times 20$ – $27\mu$ ; aplanospore  $11$ – $14\mu \times 28$ – $34\mu$ .

This species is to be compared with *Mesotaenium chlamydosporum* forma *minor* W. & G. S. West. In the vegetative condition it will doubtless be difficult to distinguish the one from the other although the diameter of the vegetative cells of West's forma *minor* is somewhat less than that of *aplanosporum*. In their monograph (the British Desmidiaceae, West, W. & West, G. S. 1904) the Wests give  $10\mu$  as the maximum width for their form while the minimum width observed in *aplanosporum* was  $13\mu$ . Therefore the chief diagnostic character is the ornamentation of the zygospore wall.

The outer spore wall of forma *minor* according to West is involucrate while in *aplanosporum* it is densely and irregularly papillate. Otherwise the zygospores are comparable.

During July of 1932 a collection of algae was taken from a dripping sandstone cliff of the Blackhand Conglomerate Formation in Jackson County, Ohio. The summer had been exceedingly hot and dry, but due to seepage springs and a northern exposure, the face of the cliff remained covered with a thick gelatinous layer of microscopic organisms. A number of samples were taken with the supposition that they might contain some members of the genus *Mesotaenium* or *Cylindrocystis*. This material upon examination proved to be almost a pure culture of a single species of

<sup>1</sup> Paper from the Department of Botany, Ohio State University, No. 381.



*Mesotaenium*, which was tentatively identified as *Mesotaenium mirificum* Archer. This identification was later questioned when a close examination revealed the true cell shape to be oblong-cylindrical and not elliptical as in *M. mirificum*. Also the unusual abundance of zygospores in all stages of development warranted a thorough investigation, because sexual spores are not common in this genus. As a result, *Mesotaenium aplanosporum* including the major part of its life history has been described.

Vegetative cells were abundant in all stages of maturity, ranging from short angular cells immediately following fission, to the elongated, slightly curved cylindrical form characteristic of the mature condition. As in most cases where cells are surrounded by a gelatinous matrix more or less distortion was evident.

Conjugating cells depicting the various stages in zygospore formation were exceptionally numerous. Although conjugation more often occurred through a tube from the middle of contiguous sides of conjugating cell pairs, it also took place from the apices of both cells, or from the apex of one cell and the middle of the other cell. A continuous tube, formed by the coalescence of thin walled processes from each cell, connected the gametangia. Fusion of the gametes occurs in the tube where the zygospore evidently remains for some time after maturity, as many old spores were found which had the empty gametangia still attached. Conjugation involving more than two cells was not observed.

The zygospores are not characterized by any one definite shape, although the globose or ovoid-globose form is the more constant and is described as the true type of spore for this species. In its variations it may be elongate-ovoid, ovoid with a constricted median portion, ovoid with an inflated median portion, or in some instances almost rectangular with slightly inflated angles.

The outer wall of the zygospore is densely covered with small rounded protuberances which are nearly circular in outline, and which have no definite arrangement. This type of spore marking is by no means common, and will doubtless be the most constant character by which this species may be identified. The color at maturity is dark red-brown.

During germination the outer ornamented spore wall splits and the contents surrounded by the colorless inner wall escape (fig. 10). Immediately following its escape from the spore wall the cell divides once forming two small cells (fig. 11) which then grow into normal individuals. Due to the fact that these spores are embedded in a common gelatinous matrix which naturally offers a good deal of resistance to the movement of any cell embedded in it, and moreover as these cells (figs. 10, 11) are always

in close proximity to the empty spore wall, it is almost a certainty that they represent the contents of that spore.

By far the most interesting discovery connected with this life history was the finding of aplanospores. Such asexual spores, while common in the Zygnemataceae, have with one exception (Archer, 1864), as far as I have been able to ascertain from the literature at hand, never been reported from the Mesotaeniaceae, and in only two or three instances in the closely allied family, the Desmidiaceae.

In relation to the number of zygosporos present, the aplanospores must necessarily be designated as rare in occurrence. However, several were found both in immature and mature condition.

At this point it may be well to digress momentarily in order to present the writer's concept of an aplanospore. This concept is essentially that of Dr. E. N. Transeau formulated in his studies on the Zygnemataceae. An aplanospore is an asexual spore formed by the secretion of a distinct wall about the contents of a vegetative cell within the original wall. This spore wall may or may not be ornamented. If ornamented the ornamentations coincide exactly with those of the zygosporos wall.

In this material it was found that the contents of certain isolated cells were enclosed by another well differentiated wall inside the original cell wall. At first this inner wall was smooth and colorless and relatively thin. Later on it became thicker and acquired the papillate condition of the mature zygosporos walls. In this spore the papillae are arranged in parallel, transverse rows. Shortly after the papillae become evident the wall takes on the reddish-brown tint which deepens until at maturity the color corresponds to that of the mature zygosporos. In the mature condition the two walls are easily distinguishable, the previously described spore wall being surrounded by the delicate, colorless cell wall. There was no evidence in any case where aplanospores were forming or had reached maturity, that conjugation had occurred. As was always the case with the zygosporos there were no empty gametangia in close proximity to these spores. As previously mentioned, the cells containing aplanospores were isolated individuals which had reached the mature condition as evidenced by cell shape and structure.

Germination of aplanospores was not observed, and although any theory which the writer may hold in regard to the germination of these spores must necessarily remain mere speculation, it seems possible to predict with some assurance their method of germination by comparison with that of aplanospores in the Zygnemataceae. In a genus such as *Zygnema*, where aplanospore germination has been studied by Transeau, the con-

tents of the spore, following the rupture of the spore wall, act as a vegetative cell and undergo division, resulting in a new filament. In all probability aplanospore germination in this *Mesotaenium* is similar to that in *Zygnema*, whereby the contents of the ruptured spore wall act as a vegetative cell.

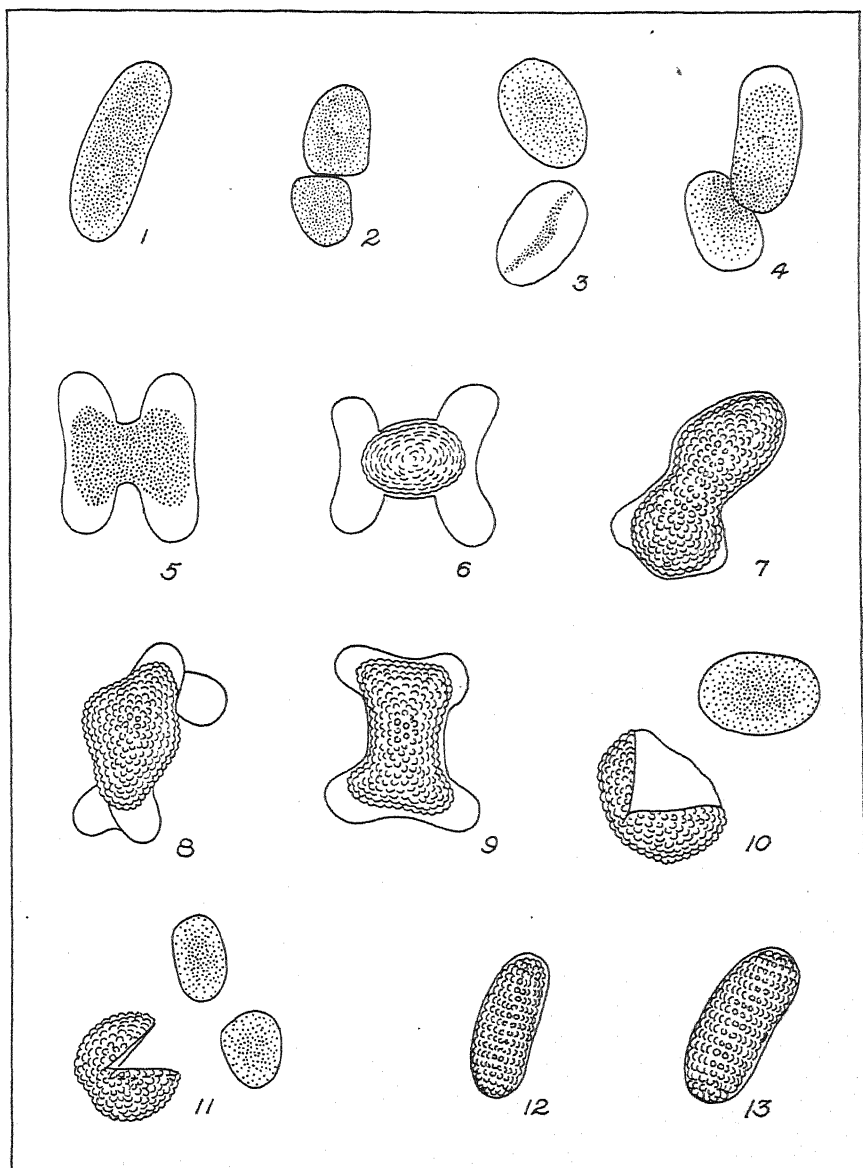
The exception previously mentioned in connection with the finding of aplanospores was *Mesotaenium mirificum* Archer (1864) in which he described asexual spores. These spores were formed by the secretion of a heavy wall about the contents of a vegetative cell after its escape through a pore which had formed in the original cell wall.

Although such spores do not correspond exactly to the writer's definition of an aplanospore, it was thought best to retain the terminology as suggested by Smith (1933) until more information pertaining to these spores can be obtained. Until such information is available it will be necessary to consider the formation of aplanospores in the Mesotaeniaceae as occurring either within the vegetative cell wall or after the contents have escaped.

I wish to express my appreciation to Dr. E. N. Transeau of this Department for his suggestions and assistance throughout the preparation of this Life History. Also to the other members of the Department who have helped in various phases of the work. To Mrs. Taft I am indebted for the drawings of the mature spores.

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Figures showing the life history of *Mesotaenium aplanosporum* sp. nov.

Fig. 1. Vegetative cell.

Figs. 2, 3. Vegetative multiplication.

Figs. 4, 5. Early stages during conjugation.

Fig. 6. Immature zygospore of the ovoid type.

Figs. 7, 8, 9. Common forms of mature zygospores.

Figs. 10, 11. Germinating zygospores.

Figs. 12, 13. Mature aplanospores formed within the old vegetative cell wall.



## A revision of the *Phacelia crenulata* group for North America

JOHN W. VOSS

Under the supervision of Dr. Philip A. Munz, at Pomona College, I have had the privilege of studying this group of *Phacelias*. I am much indebted to him for his kind help and suggestions, and I am indebted also to the curators of herbaria loaning material for this work. These herbaria are cited in this paper with the abbreviations as follows:

New York Botanical Garden (N),  
Gray Herbarium of Harvard University (G),  
University of California (C),  
Pomona College (P),  
Rancho Santa Ana (S.A.)

I have also had types and special material from:

United States National Herbarium (U.S.)  
University of Utah (U),  
California Academy of Sciences (C.A.),  
Rocky Mountain Herbarium, University of Wyoming (R.M.),  
Herbarium of Mr. G. L. Osterhout of Windsor, Colo. (Ost.)

The treatment of this group by Brand in *Das Pflanzenreich* IV, 251: 73-85, 1913 is entirely inadequate, being unsatisfactory by reason of its inaccuracies and omissions. Macbride in *Cont. Gray Herb.* 49: 24-26, 1917 has made several helpful contributions to and modifications of Brand's work, but these of course, cover only a few species.

This group of resinous, glandular *Phacelias* is differentiated primarily on the basis of seed characters. The seeds are somewhat cymbiform, favose-reticulate or pitted over the entire surface; the ventral side being characterized by a central, longitudinal salient ridge.

### KEY CHARACTERS AND CRITERIA FOR DIFFERENTIATING ENTITIES

*Growth habit.* For the most part the habit of growth is erect, with moderate branching from base. In a few instances, however, this type is modified and the habit becomes useful as a key character. *P. Popei* and its varieties are examples of one kind of modification; all branching is at the base, and in one variety the stems may be erect while in another, the stems are decumbent. Another variation is such as is found in *P. glandulosa* where the plant is characteristically unbranched, the stem stout, terete and erect, with a cluster of basal leaves and terminating at the top in a crowded spicate thyrsum.

*Leaves.* Though not particularly good as key characters, due to the

variability caused by environmental and distributional factors, the leaves are often useful for tentative determination of species, and in some cases, varieties. Size is not particularly valuable, but the general shape of the leaves, the type and fineness of dissection, the character of the margin, and distribution of leaves on the plant are all more or less diagnostic factors. Plants with finely divided leaves tend to be more finely dissected in the southern part of their range. This characteristic is particularly well displayed by *P. neomexicana*, and to some degree by *P. Popei*.

*Pubescence.* Though not particularly satisfactory as a key character, in a few instances it had to be used as such. In such cases a comparatively large amount of intergradation is found, for example, in *P. crenulata* var. *ambigua*, where the differentiation of this entity is dependent upon whether or not the stem and midribs are setose-hispid; the plants from the Colorado Desert are conspicuously so. To the north, however, the plant is more sparsely setose, and the hairs are not as long. Of course as this tendency increases the distinction between var. *ambigua* and var. *typica* becomes more and more difficult. A like condition exists in *P. congesta*; the western form of the plant is characterized by its silvery pubescence and is known as var. *rupestris*, while var. *typica*, the eastern form, is lacking in this indumentum. In the intermediate region are found both *rupestris* and *typica* and their intergrades.

*Inflorescence.* The disposition of the scorpioid racemes into clusters and the habit of these clusters are of determinative value in a few instances. *P. glandulosa*, *P. utahensis*, and *P. texana* are outstanding with their spicate thyrsus. *P. crenulata* var. *funerea* is marked by the loosely paniculate grouping of these clusters, while in varieties *ambigua* and *typica* the grouping is rather cymose.

*Corolla.* The size and particularly the shape of the corolla are of considerable importance diagnostically. In a number of the species the corolla size is very constant throughout, and can be relied upon in cases where used as a key character. The shape of the corolla is used in distinguishing between two large groups, one with corolla tubular the other with corolla campanulate or rotate campanulate. In a few cases this is a nice distinction, nevertheless a good one.

*Appendages in corolla.* With one exception, the size, shape and position of the appendages at the base of the stamens in the corolla are of little value as a determinative character. There is a great range of variability in even a given variety. The one exception is found in *P. denticulata*, which plant has a pair of tiny spike-like appendages protruding into the corolla at the base of each stamen.

*Stamens.* In most cases the relative length of the stamens is a constant

character within limits such as are described by the terms, "included," "equaling," "barely exceeding," "exserted less one half the length of the corolla," or "more than one half the length of the corolla."

*Seeds.* Characters exhibited by the seeds I consider to be the most significant and diagnostic of all. Divergent tendencies seem most quickly evidenced in a modification of their size, shape or marking, and yet at the same time, within a given species, the variations are sufficiently slight as to make them extremely usable key characters.

Typically, the seed is oval to narrowly oblong, often somewhat cymbiform with the entire surface foveolate, and ventral surface divided longitudinally in the center by a salient ventral ridge. Modifications which may appear and are diagnostically useful comprise the following:

1. Ventral surface may, or may not be excavated on either side of salient ventral ridge. The most common condition is that displaying excavation. The other type is illustrated by *P. Bakeri* where the raphe is elevated on this salient ridge above the rounded unexcavated ventral surface.
2. Length of the seed may vary with different entities.
3. Ventral surface of the seed may be marked by transverse tubercle-like rows or corrugations.
4. Dorsal surface of the seed may be emarginate with a light colored, glutinous, thickened band. This character is of little determinative value.

#### KEY TO SPECIES

1. Stamens included.
  2. Stem reddish; seeds corrugated. Southern Nevada to Western Texas.....1. *P. coerulea*
  2. Stem green; seeds not corrugated.
    3. Leaves not more than once pinnatifid; seeds 3 mm. long or less; corolla appendages oblong. Southwestern Nevada.....2. *P. Anelsoni*
    3. Leaves twice pinnatifid; seeds 4 mm. long or more; corolla appendages spike-like. Colorado and Wyoming.....3. *P. denticulata*
1. Stamens exserted.
  2. Corolla tubular.
    3. Seeds not corrugated. New Mexico, Oklahoma, and Texas.....4. *P. integrifolia*
    3. Seeds corrugated.
      4. Plant viscid. Arizona.....5. *P. serrata*
      4. Plant cinerous pubescent. Southern Utah and Nevada.....6. *P. Palmeri*
  2. Corolla campanulate.
    3. Seeds without transverse corrugations on ventral side.
      4. Corolla lobes fimbriate, dentate or crenulate.
        5. Seeds more than 2.5 mm. long; stem branching throughout.....7. *P. neomexicana*
        5. Seeds less than 2 mm. long.
          6. Stem simple, erect. Central Mexico.....8. *P. Coulteri*
          6. Stem branching at base only. Northern Mexico, northward.....9. *P. Popei*
      4. Corolla lobes entire, or nearly so.
        5. Ventral surface of seed not excavated on either side of salient ridge. Western Colorado and adjacent Utah.....10. *P. Bakeri*



5. Ventral surface of seed excavated on each side of salient ridge.
  6. Seeds 2 or 4, less than 2.5 mm. long. Texas, New Mexico, and Arizona.
  7. Seeds over 2.25 mm. long, leaves coarsely pinnatifid. .... 11. *P. congesta*
  7. Seeds less than 2.25 mm. long; leaves finely pinnatifid. .... 9. *P. Popei*
  6. Seeds 4, over 2.5 mm. long. Colorado, northward.
    7. Corolla 7 mm. wide or more; seeds over 3.5 mm. long. .... 12. *P. splendens*
    7. Corolla not over 6 mm. wide; seeds less than 3 mm. long.
      8. Leaves not pinnate, merely dentate. .... 13. *P. utahensis*
      8. Leaves pinnate.
        9. Leaves bipinnately divided. Jackson County, Colorado. ....
        - ..... 14. *P. formosula*
        9. Leaves once pinnate. Wyoming, Montana, Idaho. .... 15. *P. glandulosa*
3. Seeds transversely corrugated on ventral side.
4. Corolla 5 or more mm. wide.
  5. Sepals scarious, especially in fruit.
    6. Sepals one to two and one half times as long as broad. .... 16. *P. scariosa*
    6. Sepals three or more times longer than broad. .... 17. *P. pedicellata*
  5. Sepals not scarious
    6. Seeds 3.5-4 mm. long. Utah and Western Colorado. .... 18. *P. corrugata*
    6. Seeds 3 mm. long or less.
      7. Leaves orbicular, sub-cordate at base. Utah. .... 19. *P. orbicularis*
      7. Leaves oblong or lanceolate, at least basal leaves over twice as long as broad.
        8. Seeds 2.5 mm. long or less.
          9. Corolla 5-6 mm. long. New Mexico, Arizona, southern Utah. ....
          - ..... 20. *P. intermedia*
          9. Corolla 7-8 mm. long. Texas. .... 21. *P. texana*
          8. Seeds 3 mm. long or more. California, Arizona, Nevada. .... 22. *P. crenulata*
  4. Corolla less than 4 mm. wide. Southern California. .... 23. *P. minutiflora*

## TREATMENT OF SPECIES

1. PHACELIA COERULEA Greene, Bull. Torrey Club 8: 122. 1881. *P. invenusta* Gray, Proc. Amer. Acad. 20: 303. 1885.

Annual, 1.5-4 dm. high; stems slender, erect, simple or occasionally branching from base, setose-hispid, glandular; leaves ovate to oblong-ovate, 3-8 cm. long, 1-2.5 cm. wide, upper strongly sinuate above, lower pinnately cleft or divided; upper leaves smaller, more ovate and with shorter petioles, finely hispid to almost viscid-villous, darkly glandular in age, nearly silvery when young; inflorescence irregular, 2 to 5 racemes in a group, terminal, usually loosely paniculate, less often cymose; scorpioid racemes compact, tightly curled in flower, loosening in fruit, 5-10 cm. long; flowers nearly sessile, the pedicel not over 1 mm. long, even in fruit; sepals lanceolate or narrowly elliptical, three-fourths as long as corolla, equalling or exceeding capsule; corolla blue or white, campanulate, 3-4 mm. long, 3-4 mm. wide, cleft nearly half way; lobes entire; appendages lunate, often auriculate at top, 0.5 mm. long, 0.1-0.2 mm. broad, attached about 0.5 mm. from base of corolla; stamens included, 2-3 mm. long; anthers ovate, small; style equalling stamens; seeds 4 in capsule, elliptical, 2-3 mm. long, 1-1.5 mm. wide; ventral surface excavated and divided by salient ridge, transversely corrugated; dorsal surface favose-pitted, often emarginate with thicker, light colored edge.

Type. Greene does not cite specimens on which he bases his description published in Nov. 1881. Since he had collected the plant on "Bluffs of the Gila," in New Mexico on April 23, 1881, I hereby designate the Greene specimen of that date at Gray Herbarium as the type. The range of this species is southern Nevada, Arizona, southwestern New Mexico, Chihuahua and adjacent Texas. Specimens seen: UNITED STATES, NEVADA: Good Springs, Clark County, *Jones in 1905* (P). ARIZONA: Peach Springs, *Jones in 1884* (P, G); Clifton, *Davidson 152* (P); Hualpai Mts., *Jones in 1903* (P); Sierra Tucson, *Pringle in 1884* (G, N); Foothills, Santa Rita Mts., *Shear 4197* (N); Skull Valley, *Jones in 1903* (P); Continental, Pima County, *Harrison and King 6942* (P); Nogales, *Brandeggee in 1892* (C); Oak Creek, above Cornville, *W. W. Jones 340* (G); Patagonia Mts., *Lemmon 84 & 121* (G); NEW MEXICO: Organ Mts., Dona Ana County, *Woolon, May 3, 1903* (P, C), *Wright 1579* (G); between Silver City and Fort Bayard, *Eastwood 8302* (P, G); 1 mile west of Hillboro, Sierra County, *Metcalf 1543* (P, N, G); Bluffs of the Gila, *Greene on April 23, 1881, type* (G). TEXAS: near El Paso, *Thurber 11* (G); El Paso, *Jones* (P); Fort Bliss, *Mrs. Clemens April 18, 1917* (P); "Texas" *Le Roy* (N). MEXICO: CHIHUAHUA: vicinity of Santa Eulalia, *Palmer 129* (G); near Paso del Norte, *Pringle 93* (G); valley of Rio Piedras Verdes, near Juarez, *Hartman 646* (G, C).

The seeds of *P. coerulea* as described by Greene may have been depauperate, or else some error occurred to cause him to record them as being "—barely one-third as large as in *P. crenulata*, almost linear in shape,—." I agree with Dr. Gray in Syn. Fl. II, 1, Suppl. 414, 1886 that the seeds are much like those in *P. crenulata* in both size and shape, and that *P. coerulea* and *P. invenusta* are identical. The characters on which Mr. Jones insists (Cont. Western Bot. 12: 52, 1908), as showing *P. invenusta* and *P. coerulea* (which he spells "*caerulea*") to be separate entities, are all such as are extremely variable even in a single plant; and in a series of specimens, though tendencies in either direction may be found for specific characters, the differences are largely ecological.

## 2. PHACELIA ANELSONI Macbride, Cont. Gray Herb. 49: 26. 1917.

Annual, 2 to 4 dm. high; stem erect, simple, terete, viscid, moderately covered with bronish glandular pubescence; leaves 2–10 cm. long, 1–2 cm. wide, narrowly oblong to nearly spatulate, pinnately cleft or parted, covered with a fine glandular pubescence, such as that on the stem but slightly more abundant; pinnae tending to be reduced toward base of leaf, margins crenate; inflorescence paniculate to racemose, terminal on main stem, occasionally on small lateral branches; scorpioid racemes loosening but little in fruit, 1.5–3 cm. long; pedicel to 2 mm. long; calyx-lobes oblanceolate, 3–4 mm. long,

1-1.5 mm. wide, puberulent, often glandular, about half as long as corolla and slightly exceeding capsule; corolla rotate-campanulate, blue or violet, 6 mm. long, 6 mm. wide; appendages in corolla lunate, 0.75 mm. long, 0.25 mm. wide, narrower at top than at bottom; stamens included; style as long or nearly as long as stamens; capsule 2.5-3 mm. long, oval, glandular, puberulent at top; seeds 3.25 mm. long, 1.25 mm. wide, quite thin, accentuating prominence of salient ventral ridge, favose-pitted, but not corrugated; ventral ridge strongly alveolate.

Type locality, Meadow Valley Wash, Nevada. Range, southeastern Nevada, from 3000 to 4500 feet. Specimens seen: NEVADA: Meadow Valley Wash, *Goodding 635*, type (R.M.); Calientes, *Jones on April 29, 1904* (G, P); Meadow Valley Wash, mile 16, *Jones on April 28 1904* (P); 12 miles south of Searchlight, *Jaeger, March 27, 1924* (P).

A distinctive plant easily separated from *P. denticulata* by the lunate appendages in the corolla and by the smaller seeds, and from *P. coerulea* by its lack of corrugations in the seed and by its larger flowers. All three species, of course, have included stamens.

3. *PHACELIA DENTICULATA* Osterhout, *Torreyia* 16: 70. 1916.

*P. glandulosa* Nutt. subsp. *eu-glandulosa* Brand var. *australis* Brand, *Pflanzenreich* IV, 251: 82-83. 1913. in part. *P. glandulosa* Nutt. subsp. *eu-glandulosa* Brand, l.c. *P. neomexicana* Thurber and Torr. var. *miophylla* Brand, l.c. p. 84.

An erect, usually simple, viscid, slightly hispid, heavily stipitate-glandular annual; stem terete, often stout, 2-4 dm. high, usually greenish, sometimes darkened by stipitate glands; leaves oblong-lanceolate in outline, 3-7 cm. long, 1-3 cm. broad, lower and more fully developed are pinnately divided, upper and very young tend to be only pinnately cleft or coarsely serrate; pinnae irregularly pinnately cleft, 1-2 cm. long, 0.4-1 cm. broad, 5-15 in number; inflorescence terminal, cymose; scorpioid racemes uncoiling as flowers mature, becoming 4 or 5 cm. long in fruit; flowers often nearly sessile; pedicel elongating to as much as 3 mm. in fruit; sepals oblanceolate, one-half as long as corolla, elongating to barely exceed capsule; corolla tubular, 5 mm. long, 3 mm. wide, apparently white or very pale blue or violet, lobes very short, margin irregularly fimbriate; appendages in corolla tiny spike-like projections, nearly filiform, about 0.25-0.5 mm. long, attached about 0.5 mm. from bottom of corolla; stamens barely included; style included; capsule ovoid-globose, 5 mm. long, 4 mm. thick; seeds 4, favose-pitted, flattened, elliptical, the only slightly excavated ventral face divided by prominent salient ridge.

Type locality, The Glades, Owl Canyon, between Fort Collins and Livermore, Larimer County, Colorado. Range, east slope of the Conti-

nental Divide in Colorado and southern Wyoming, 5000 to 9000 feet. Specimens seen: COLORADO: The Glades near Owl Canyon, Larimer County, *Osterhout* 5233 type coll. (N, this sheet wrongly numbered 5238, fide letter from Osterhout); Georgetown, *Jones* 511 in part (P, N); La Porte, Larimer County, *Cowen* on June 1, 1895 (N); Salida, *Baker, Earle, and Tracy* 20 (N, G, P); near Mt. Harvard, *Shear* 3306 (N); Trinidad, *Tracy* 14 (N), *Beckwith* 137 (N); Cripple Creek, *Eastwood*, on Aug. 5, 1897 (N); Walsenburg, *Rydborg and Vreeland* 5754 (N); near Palmer Lake, *Woodward* on July 29, 1883 (G); Golden City, &c., *Greene* in 1870 (G); Clear Creek Canyon at Dumont, *Patterson* 107 (G). WYOMING: Laramie Hills, Albany County, *A. Nelson & E. Nelson* 6859 (N, G); Laramie Hills, *A. Nelson* 9566 (N, G); Pole Creek, *A. Nelson* 1361 (G, N); Jaw-bone Gulch, *E. Nelson* 2030 (P).

A comment on the miserable treatment of this very good species by Brand will be taken up more fully in the discussion under *P. glandulosa*. *Nelson* 8053 is *P. neo-mexicana* Thurber, var. *alba* (Rydb.) Brand at (G and P), but *P. denticulata* at (N). In regard to the specimen of *P. denticulata* labeled "The Glades, near Owl Canyon, Larimer County, *Osterhout* 5238, June 18, 1915 (N)," I have the following word from Mr. Osterhout under date of Oct. 26, 1934: "For *Phacelia denticulata* the correct No. is 5233. I have collected it in other localities, but only once on June 18, 1915."

4. *PHACELIA INTEGRIFOLIA* Torr., Ann. Lyc. New York 2: 222, t.3. 1826.

*P. arenicola* Brandege, Univ. Calif. Pub. Bot. 4: 185. 1911. *P. integrifolia* Torr. var. *arenicola* (Brandegee) Brand, Pflanzenreich IV, 251: 82. 1913.

Plant an erect annual or biennial, glandular, viscid, hispidulous to nearly hispid; stem simple or branching from base, sometimes of a brownish color due to profuse fine glandular pubescence; leaves 2-15 cm. long, 1-7 cm. wide, varying from oblong to ovate, pinnately cleft or usually merely deeply crenate, lower sometimes cordate or truncate at base, upper short petiolate or sometimes nearly amplexicaul; inflorescence loosely paniculate; scorpioid racemes 2-4 cm. long in terminal clusters, loosening slowly, but reaching a length of 6-12 mm. in fruit, calyx lobes broadly oblanceolate, hirsute, about half as long as corolla and barely exceeding capsule; corolla tubular, pale, 5-6 mm. long, limb 3 mm. wide; appendages in corolla short, nearly as broad as long; stamens and style exserted 3 mm. or more; capsule ovoid-globose, 3.5 mm. long, seeds faveolate, 3 mm. long, 1.5 mm. wide, ventral surface excavated, salient ridge somewhat scurfy, dorsal surface often emarginate.

KEY TO VARIETIES OF *PHACELIA INTEGRIFOLIA*

- Basal leaves less than 3.5 mm. wide. Oklahoma, Texas, New Mexico & northeastern Mexico. . . .  
 . . . . . 4a. var. *typica*  
 Basal leaves 4 mm. wide or more. Mountains of southwestern Texas. . . . . 4b. var. *robusta*

4a. *Phacelia integrifolia* Torr. var. *typica* n. nom. *P. integrifolia* Torr. l.c.

Plants 1.5–4 dm. high; leaves oblong or narrowly ovate, 2–7 cm. long, 0.7–2 cm. wide, crenate.

Type locality, "On the Platte," Dr. James, June 25, 1820, Long's 1st Expedition (N). Since I have seen no material known definitely as from Colorado nor from southern Kansas, I question the James locality. Range, Kansas, Oklahoma, western Texas, New Mexico, southeastern Utah, Coahuila, and Chihuahua. Specimens representative: UNITED STATES: KANSAS: Gloss Mts., *White on July 13, 1899* (N). OKLAHOMA: Fair Valley, Woods County, *Stevens 1636* (G, N). TEXAS: Plains west of Pecos, *Tracy & Earle 417* (N); Kent, *Tracy & Earle 390a* (G, N); Indian Hot Springs, *Jones 25744* (P); El Paso, *Thurber 183* (G, N), *Jones 3712* (C, P); Franklin, *Lemmon 242* (G); Estelline, *Reverchon 3890* (G); Findlay, *Jones 28500* (C, P). NEW MEXICO: Hop Canyon, Magdalena Mts., *Diehl 874* (P); near Espanola, Santa Fe County, *A.A. & E.G. Heller 3545* (G, N, P); Las Vegas, *Osterhout 7039* (P); Magdalena, Socorro County, *Eggleston 20228* (G, N); Mesilla, Dona Ana County, *Wootton 33* (C, G, N, P); San Ysidro, *Arsène & Benedict 17617* (G); UTAH: along San Juan River near Bluffs, *Rydberg and Garrett 10,033* (N). MEXICO: CHIHUAHUA: "Sand Hills," *Thurber 758* (G, N); near Chihuahua, *Pringle 255* (G); near Paso del Norte, *Pringle 177* (G); El Toro, near Movano, *Purpus 4458* (G).

Brandege in his description of *P. arenicola* l.c. compares it to the altogether different species, *P. coerulea* with included stamens and a resemblance to *P. crenulata* in general appearance. He does not mention *P. integrifolia*.

4b. *PHACELIA INTEGRIFOLIA* Torr. var. *ROBUSTA* Macbride, Cont. Gray Herb. 49: 25. 1917.

Plant robust, 2–9 dm. high; leaves 3–15 cm. long, 3–7 cm. wide, ovate, or upper leaves sometimes nearly orbicular, crenate, or often pinnately cleft.

Type locality, Chinati Mts., Texas. Range, mountains of western Texas. Material seen: TEXAS: Chinati Mts., *Havard 250* type (G); Chisos Mts., Brewster County, *Moore & Steyermark 3232* (G, C, N), *Palmer 34077* (N).

5. *Phacelia serrata* Voss. n. sp.

Annual, 1–3 dm. high; stems erect usually simple, occasionally branching at base, setose hispid, often glandular, reddish to green, terete; leaves 1–5 cm. long, 0.5–1.25 cm. broad, lanceolate in outline, serrate, occasionally dentate, teeth somewhat rounded or blunt, most leaves at base, few smaller ones

above, hispidulous, often covered with black glandular dots, though sometimes scarcely at all glandular; petioles often up to 3 cm. long at base of plant and practically lacking at the top; inflorescence more or less paniculate to almost cymose; scorpioid racemes compact in both fruit & flower; pedicel 0.5 mm. long in flower, 1 mm. long in fruit; sepals elliptic-oblancheolate, broadening and elongating slightly in fruit, 3-4 mm. long, 0.75-1.5 mm. wide, hirsute, glandular, about one half as long as corolla, and about equaling capsule; corolla blue, tubular, scarcely any wider at the top, 2-3 mm. broad, 4-6 mm. long, lobes entire; appendages in corolla lanceolate, 0.7 mm. long, 0.25 mm. wide, broader at bottom and tapering toward top, attached along edge toward filament; stamens exerted about length of corolla; style exerted more than stamens, divided three-fourths of length; capsule oval, 3 mm. long, 2-2.5 mm. in diameter, glandular, somewhat puberulent on top; seeds 2.5-3 mm. long, 1-1.25 mm. wide, favose pitted, often emarginate, with thickened edge of lighter color on dorsal side; ventral side coarsely corrugated or undulate on margins, salient ridge prominent and somewhat corrugated on one side.

Planta annua, 1-3 dm. alta; caulibus erectis, plerumque simplicibus, pro re nata base ramosis, setis hispidis, saepe glandulosis, subrubris vel viridibus, teretibus; foliis 1-5 cm. longis, 0.5-1.25 cm. latis, lanceolatis, serratis, pro re nata dentatis, plerumque base plantae, hispidulis, saepe fulve glanduloso-punctatis; petiolis inferioribus 1-3 cm. longis superioribus deficientibus; inflorescentia paniculata aut cymosa, in fructu plerumque non elongata; pedicellis, 0.5-1 mm. longis; sepalis elliptico-oblancheolatis, in fructu aliquanto amplificatis, 3-4 mm. longis, 0.75-1.5 mm. latis, hirsutis, glandulosis; corolla subcoerulea, tubulosa, 2-3 mm. lata, 4-6 mm. longa, lobis integris; appendiculis corollae lanceolatis, 0.7 mm. longis, 0.25 mm. latis; staminibus 4-6 mm. exertis; stylo stamina paulum excedento, alto diviso; capsula ovale, 3 mm. longa, 2-2.5 mm. crassa, glandulosa, apice subpuberulenta; seminibus 2.5-3 mm. longis, 1-1.25 mm. latis, favoso-notatis, saepe emarginatis, dorso cum margine incrassata et pallida, ventro cum facie crasse corrugata vel cum marginibus undulatis, fastigo saliente prominente et subcorrugato.

Type, San Francisco Mts., Arizona, *Purpus 8064* (Pomona College Herbarium No. 200561; isotype at Univ. of Calif.) Range, San Francisco Mts., Arizona. Specimens seen: ARIZONA: volcanic scoria, San Francisco Mts., n. Arizona, *Lemmon & Wife in Sept. 1884* (C); vicinity of Flagstaff, *MacDougal 288* (C, G, N, P); *Palmer 335* in part (G, N); Sunset Mt., Flagstaff, *Rusby on Aug. 21, 1915* (N).

6. PHACELIA PALMERI Torr., Watson, Bot. King Exped., 251. 1871.

Erect biennial, 2-8 dm. high, leafy at the base, more sparsely so above; herbage covered with a cinerous-glandular tomentum intermixed with a hispid or hispidulous indumentum, gray-green to olive-green; stem stout, terete, usually unbranched, except perhaps toward the base, where a few short

branches terminating in dense clusters of scorpioid racemes may occur; leaves oblong-lanceolate, irregularly dentate or serrate, or at times sinuate or crenate, 2–10 cm. long, 0.5–3 cm. broad, lower petiolate, upper often amplexicaul, at least sessile; inflorescence a spicate thyrsus 5–30 cm. long; scorpioid racemes compact, soon loose, 2–7 cm. long in flower, elongating slightly in fruit; pedicels less than 1 mm. long; calyx-lobes oblanceolate, half as long as corolla, a little longer than the capsule; corolla pale, tubular, 5–7 mm. long, 3 mm. wide, appendages in corolla narrowly lunate, acuminate at top, attached about 1 mm. from base of corolla; stamens and style exserted 5–7 mm.; capsule ovoid-globose 4–4.5 mm. long, 3 mm. thick; seeds 4, 2–4 mm. long, faveolate, ventral surface transversely corrugated, and excavated on either side of salient ridge.

#### KEY TO THE VARIETIES OF PHACELIA PALMERI

1. Seeds 2–2.5 mm. long. .... 6a. var. *typica*
2. Seeds 3–4 mm. long. .... 6b. var. *foetida*

#### 6a. *Phacelia Palmeri* Torr. var. *typica* Voss n. nom.

*P. Palmeri* Torr., l.c. *P. integrifolia* Torr. var. *Palmeri* Gray, Proc. Amer. Acad. 10: 318. 1875.

Leaves usually less than 6 cm. long, sinuate or crenate; seeds 2–2.5 mm. long.

Type locality, near St. George, on the Rio Virgin in southern Utah. Range, southern Utah and northern Arizona. Specimens seen: UTAH: near St. George, on the Rio Virgin, *Palmer 4, in 1870* type (N); southern Utah, *Bishop in 1874* (P); St. George, *Craig 1397* (P); St. George, *Palmer 335* (G); Diamond Valley, *Purpus 6191* (C), *6158* (C); Cedar Canyon, Iron Co., *Garrett on Sept. 3, 1921* (U). ARIZONA: Mociac, Coconino Co., *Cottam 4113* (P).

6b. *PHACELIA PALMERI* Torr. var. *FOETIDA* (Goodding) Brand, Das Pflanzenreich IV, 251: 79. 1913. *P. foetida* Goodding, Bot. Gaz. 37: 58. 1904.

Leaves to 10 cm. long, margins usually dentate or serrate, sometimes crenate; seeds 3–4.5 mm. long.

Type locality, laval fields of southern Utah. Range, southern Utah, Nevada and northern Arizona. Specimens seen: UTAH: southern Utah, *Parry 176* (G, N); St. George, *Palmer + 335 in part* (G). NEVADA: Frenchman Mt., northeast of Las Vegas, *Munz 12971* (P); Mesquite Well, *Goodding 2270* (C). ARIZONA: Lee's Ferry, *Jones on June 16, 1890* (P).

7. *PHACELIA NEOMEXICANA* Thurber ex. Torr., in Bot. Mex. Bound. Surv., 143. 1859.

Annual, branching throughout, or branching only at base, or sometimes simple, erect, viscid-villose, often heavily stipitate-glandular; leaves opposite

or alternate, occasionally axillary, ovate or lanceolate, 4-10 cm. long, 2-4.5 cm. broad, once or twice pinnately parted or divided; scorpioid racemes loosening in fruit; pedicels not over 1.5 mm. long even in fruit; calyx-lobes lanceolate or spatulate, half to three-fourths as long as corolla, about 1 mm. broad, rather glandular; corolla white, blue or violet, campanulate, 4-5 mm. long, 3-4 mm. wide, lobes fimbriate, or dentate; appendages in corolla lunate, 0.75 mm. long, 0.5 mm. wide, attached about 0.5-0.75 mm. from base of corolla; stamens and style exerted 1-4 mm.; seeds 2.5-3 mm. long, finely alveolate, ventral surface excavated and divided by salient ridge.

#### KEY TO VARIETIES OF PHACELIA NEOMEXICANA

1. Plant erect, usually branching throughout.
  2. Stamens exerted  $\frac{1}{4}$  length of corolla; corolla blue.....7a. var. *eu-neomexicana*
  2. Stamens exerted  $\frac{1}{2}$  length of corolla or more; corolla white.....7b. var. *alba*
1. Plant branching at base only.....7c. var. *pseudo-arizonica*

7a. *PHACELIA NEOMEXICANA* Thurber var. *EU-NEOMEXICANA* Brand, Pflanzenreich IV, 251: 83. 1913.

*P. neomexicana* Thurber ex. Torr. in Bot. Mex. Bound. Surv., 143. 1859. in part. *P. glandulosa* Nutt. var. *neomexicana* Gray, Proc. Amer. Acad. 10: 319. 1875.

Stems somewhat thin but erect, simple, 3-4 dm. high, covered with a silvery setose-hispid pubescence, often reddish and glandular beneath the short bristles; leaves opposite or alternate, 5-10 cm. long, 2-4 cm. broad, ovate, pinnately divided 5-9 times, finely hispidulous so as to appear silvery-green; pinnae deeply serrate or incised, 1-3 cm. long, 0.75-1.5 cm. wide; inflorescence terminal or arising from axils of upper leaves, giving a paniculate effect, racemes 2-6 cm. long; pedicels to 1 mm. long in fruit; sepals 3-4 mm. long, 1 mm. broad, about  $\frac{1}{4}$  as long as the corolla and slightly exceeding the capsule, hispidulous and quite glandular; corolla blue or purple, 4-5 mm. long, 3 mm. wide; stamens exerted 1 mm.; anthers small; style exerted almost as far as stamens, cleft three-fourths of length; capsule globose, 3-3.5 mm. in diameter, sparsely hispidulous at base, becoming more so at top with style often persisting; seeds 3 mm. long. 1.5 mm. wide.

Type locality, Pine Woods, Santa Rita (Copper Mines), Grant Co., New Mexico. Range, southwestern New Mexico. Specimens seen: NEW MEXICO: Copper Mines, *Wright 1577* (G, N), *Thurber 1111* type collection (N, G); Hillsboro Peak, Grant County, *Metcalf 1506* (G); Bear Canyon, north of Fierro, *Diehl in 1903* (P).

7b. *PHACELIA NEOMEXICANA* Thurber var. *ALBA* (Rydberg) Brand. Pflanzenreich IV, 251: 83, 1913.

*P. alba* Rydberg, Bull. Torrey Club 28: 30. 1901. *P. neomexicana* Thurber, var. *Coulteri* sub. var. *foliosissima* Brand. l.c., 84.

Stem simple, or branching freely throughout, 1.5-4 dm. high, erect or



ascending, hispid to villous, heavily stipitate-glandular, especially above; leaves ovate, 4–8 cm. long, 2–4.5 cm. wide, irregularly bipinnate, usually viscid-villous, darkly glandular, occasionally only hispidulous; inflorescence dense, branched, corymbose to spiciform; scorpioid racemes about 2 cm. long in flower, lengthening to as much as 9 cm. in fruit; pedicels to 1.5 mm. long, lengthening only in fruit, flowers being sessile; calyx-lobes lanceolate or spatulate, two-thirds as long as corolla, about equalling capsule, viscid-villous or hispidulous; corolla white; stamens conspicuously exerted about 3 mm.; style exerted; seeds 2.75–3 mm. long, 1–1.3 mm. broad.

Type locality, Sangre de Cristo Creek, Colorado. Range, on the Continental Divide from Wyoming to Mexico. Specimens seen: WYOMING: Jelm, Albany County, *A. Nelson 8053* in part (G, N, P). COLORADO: road to Wagon Wheel Gap Experiment Station, Mineral County, *J. Murdock Jr., 4645* (P); Doyles, *Baker 634* (P, G); Georgetown, *Jones 511* (in part) (P); Clear Creek Canyon, Georgetown, *Patterson 106* (G); Clear Creek and alpine ridges east of Middle Park, *Parry 314* (G), Crestons, *Brandegree in 1877* (C). UTAH: Fish Lake around Twin Creeks, *Rydberg and Carlton 7498* (N, G); Loa, *Jones 5639 c* (P); Panguitch Lake, *Jones 6015ai* (P). NEW MEXICO: Vermejo Park, *Mrs. O. St. John 65* (G); near Luna, Datil Forest, Catron County, *Eggleston 20244* (G); Tularosa Creek, 3 miles south of Mescalero Agency, *Wolf 2765* (P, G); White Mountains, Lincoln County, *Wooton 230* (P, G, C); Sacramento Mountains, Cloudcroft, *Wooton on July 31, 1899* (C, P). CHIHUAHUA: near Colonia Garcia, *E. W. Nelson 6105* (G), *Townsend and Barber 129* (G, C, P); Canyon Rio San Miguel, *Hartman 651* (G).

This plant has a large range and exhibits an interesting variation in the leaf form. In the north, Wyoming and Colorado, the lobes are considerably larger than in those from New Mexico and Mexico.

7c. *Phacelia neomexicana* Thurber var. *pseudo-arizonica* (Brand) Voss n. comb.

*P. neomexicana* var. *euneomexicana* sub. var. *pseudo-arizonica* Brand, Pflanzenreich IV, 251: 83. 1913.

Stem erect, branching at the base 1 to 2 dm. high, leaves mostly basal, lanceolate, bipinnately divided, viscid-villous, moderately glandular; inflorescence cymose; scorpioid racemes in terminal clusters of 3 to 6, 1–3 cm. long, slightly longer in fruit; pedicels less than 1 mm; calyx-lobes oblanceolate, half as long as corolla, barely as long as capsule; corolla pale, 4 mm. long, 5 mm. wide, stamens exerted 3 mm. or more; style equalling stamens; seeds 2.5 mm. long, 1 mm. wide, not deeply excavated on ventral surface, margin thin, and dentate under a lens.

Type locality, Flagstaff, Arizona. Range northern Arizona and south-

ern Utah. Specimens seen, ARIZONA: near Flagstaff, *Purpus* 8030 (C, P) type at Berkeley; Bangharts Ranch, *Rusby in* 1883 (N). UTAH: southern Utah, northern Arizona, &c. *Palmer* 334 in part (N); southern Utah, *LeRoy* 334 (N).

8. *PHACELIA COULTERI* Greenman, Proc. Amer. Acad. 41: 241. 1904.

*P. neomexicana* var. *Coulteri* (Greenman) Brand, Pflanzenreich IV, 251: 84. 1913.

Annual, stem rather stout, erect, branched above, 3-4 dm. high, villous over whole darkly glandular surface; leaves 2-9 cm. long, 1-6 cm. broad, ovate, pinnately dissected into many fine segments or lobes, glandularly hispidulous giving a decided brownish color; inflorescence corymbose or paniculate; scorpioid racemes hirsute, brownish glandular, not loosening particularly in age; pedicels up to 1 mm. in length; sepals oblanceolate, one-half length of corolla, slightly exceeding capsule; corolla narrowly campanulate, 6 mm. long, 5 mm. wide, light blue or white, petals repand to fimbriate; appendages in corolla triangular, reflexed, 0.5 mm. long, 0.25 mm. broad, attached 0.5 mm. above base of corolla; stamens exerted about 2 mm.; anthers 0.3 mm. in diameter; style exerted about 2 mm.; seeds 4, 2 mm. long, 1 mm. wide, with favose pits on dorsal surface, the salient ventral ridge prominent though submerged between incurved outer edges of seed.

Type locality, fields about Buena Vista Station, Hidalgo, Mexico. Range in central Mexico. Specimens seen: HIDALGO: fields about Buena Vista Station, *Pringle* 8988, Aug. 4, 1904, type coll. (C, G); in Mexico—*Coulter* 921 (G).

This plant resembles *P. neomexicana* in external characters, except that it is not so branched. The seeds are much smaller.

9. *PHACELIA POPEI* Torr. & Gray, Pacif. Rail. Rep. Explor. Mississippi 2: 172. 1855.

Diffuse annual branching at base which is often surrounded by a cluster of basal leaves, 1-3 dm. high, viscid-pubescent with fine spreading hairs intermixed with stiffer ones on stem midribs; leaves once or twice pinnate, 2-15 cm. long, 1-3 cm. wide, narrowly oblong; pinnules linear or lanceolate, obtuse or acute; scorpioid racemes in crowded terminal clusters of 3 to 6, 1-4 cm. long in flower, lengthening considerably in fruit; pedicels less than 2 mm. long; calyx-lobes oblanceolate, 2.5-4 mm. long, seldom more than barely exceeding capsule, and about half as long as corolla; corolla blue or white, campanulate, 3.5-7 mm. long, nearly as broad as long; lobes entire, crenulate or denticulate; appendages in corolla lunate, nearly as broad as long; stamens and style exerted conspicuously; capsule globose, 2 mm. in diameter; seeds 1.75 mm. long, 1.25 mm. wide, cymbiform, ovate, favose-reticulate, deeply excavated on either side of salient ridge.

## KEY TO VARIETIES OF PHACELIA POPEI

- Corolla 6 mm. broad, blue.....9a. var. *similis*  
 Corolla 4 mm. broad, white.  
   Stems ascending.....9b. var. *typica*  
   Stems decumbent-spreading.....9c. var. *arizonica*

9a. **Phacelia Popei** Torr. & Gray. var. **similis** (Wooton & Standley) Voss  
 n. comb.

*P. similis* Wooton & Standley. Bull. Torrey Club 36: 111. 1909.

Plant often quite green; pinnules tending to be somewhat acute; corolla 6–7 mm. long, blue or violet.

Type locality, Nutt Flats, Sierra Co., New Mexico. Range, New Mexico and western Texas. Specimens seen: NEW MEXICO: Nutt Flats, Sierra Co., *Metcalf* 1565 type coll. (N). TEXAS: between Langtry and Marathon, *McKelvey* 1913 (P); between Alpine and Marfa, *McKelvey* 2010 (P); 9 miles north of Sanderson, Terrell County, *Cory* V4 (P).

9b. **Phacelia Popei** Torr. & Gray var. **typica** n. nom.

*P. Popei* T. & G., l.c.

Plant branching at base but often lacking basal leaf cluster; leaves 2–12 cm. long, 1–3 cm. wide; corolla white, 4 mm. long.

Type locality, Llano Estacado, Texas. Range, New Mexico, western Texas and adjacent Mexico. Specimens seen: TEXAS: Llano Estacado, *Captain Pope*, type (G); near Sweetwater, Nolan County, *Palmer* 33972 (G); plains west of Pecos, *Tracy & Earle* 117 (G, N); sandy plains, upper Colorado, west Texas, *Reverchon in April* (G, N); southwest Texas, *Havard* (G); Kent, *Tracy & Earle* 390 (G, N); Alpine, *Hughes* 30 (N). NEW MEXICO: *Wright* 1578 (G, N); Deming, *Jones* 25750 (P); near Fort Bayard, *Eastwood* 8299 (P, G); between Deming and Silver City, *McKelvey* 2065 (P). CHIHUAHUA: Oja de Vaca &c., *Thurber* 308 in part (G, N).

9c. **Phacelia Popei** Torr. & Gray var. **arizonica** (Gray) Voss n. comb.

*P. arizonica* Gray, Syn. Fl. II, 1: 394. 1878.

Plant tending to be sparsely leaved, except at base; corolla white, 3.5–4.5 mm. long.

Type locality, southern Arizona. Range, southern Arizona, southwestern New Mexico and adjacent Sonora. Specimens representative, ARIZONA: Tucson, *Lemmon* 169 (C, N); mesas near Tucson, *Pringle on May* 7, 1883 (N); Steins, *Jones* 28505 (P); Dragoon, *Jones* 28503 (P); Cochise, *Jones* 28502 (P); near Baboquivari Peak, *Harrison & Kearney* 8557 (P); Lowell, *Parish on May* 2, 1884 (G, N); Picacho, Pinal County, *Gillespie* 8914 (C, N); Red Rock, *Parish* 156 (G); Chase Creek, *Davidson* 1080

(G); near Williams, *Lemmon in August 1884* (C); Nogales, *Brandegees on May 24, 1892* (C); NEW MEXICO: Nutt Flats, Sierra County, *Metcalf 1564* (G, N, P); Gila River bottom near Cliff, Grant County, *Metcalf 53* (C, G, N, P); Lordsburg, *Jones 25741 and 25742* (P); near Lordsburg, *McKelvey 2082* (P). SONORA: Plains near Altair, *Pringle on April 4, 1884* (G); Las Playas, *Thurber 308* in part (G); 15 miles north of Magdalena, *Fosberg 7925* (C, P).

According to Dr. Gray in his original description of *P. arizonica* l.c. the type was collected by Thurber in southern Arizona as Thurber's name is given first. Although I have not seen this specimen I have seen Greene's collection (the second cited) and the collections of Lemmon, Pringle and Parish cited by Dr. Gray in Syn. Fl. II, 1: Suppl. 414. 1886.

10. PHACELIA BAKERI (Brand) Macbride, Cont. Gray Herb., n.s. 49: 29. 1917.

*P. crenulata* Torr. var. *Bakeri* Brand. Pflanzenreich IV, 251: 78. 1913.

Erect annual, 1.5–3 dm. high, rather densely hispidulous, the pubescence intermixed with stipitate glands and bristles arising from glands; stems branching from base, terete; leaves narrowly ovate, pinnately divided, usually 4–8 cm. long, 1–3 cm. broad; pinnae 5–9, irregularly crenate to coarsely dentate; inflorescence paniculate, occasionally nearly cymose; racemes numerous, rather compact not loosening much in age, tending to be straight rather than extremely scorpioid; pedicels 1 mm. in flower, becoming 3–5 mm. in fruit; sepals one-half as long as corolla, slightly exceeding capsule, narrowly spatulate or oblanceolate; corolla campanulate, blue or violet, 7 mm. long, 5–7 mm. wide; appendages in corolla conspicuous, triangular to broadly lunate, 1.5 mm. long, 0.5 mm. broad, attached about 0.1 mm. from bottom of corolla; stamens exserted about 7 mm.; anthers ovoid, about 0.5 mm. long; style 6–7 mm. long; seeds 3.25 mm. long, 1.5 mm. wide, occasionally very thin or almost depauperate, covered with tiny favose pits; salient ventral ridge pressed to one side.

Type locality, Ouray, Colorado. Range, western slope of Rocky Mts., Colorado, Utah, and southwestern Montana, at from 7000 to 10,000 feet. Specimens seen, COLORADO: Ouray, *Baker 758*, type coll. (P, C, G, N); Ouray, *Nelson 9812* (C); Gunnison, Gunnison County, *Munz 13060* (P); Cheyenne Canyon, *Shear 4579* (N); Divide—Cripple Creek, Teller County, *Clokey 3838* (G, N, P); west Spanish Peak, *Rydberg and Vreeland 5754* (N); Cumbres, *Baker 549* (N, P, G); head of Rio Grande, *Brandegees, Sept. 1875* (G). MONTANA: Bannock City, *Watson 281* (G). UTAH: P. V. Junction (Colton), Wasatch Mts., *Jones, Aug. 1883* (N, P). IDAHO: Clayton, Custer Co., *Macbride & Payson 3364* (G).

In Brand's description of *P. crenulata* var. *Bakeri*, the type cited by

him is the only one belonging to this group. The other specimens cited belong to different species. He has also included under *P. glandulosa* as variety *australis* material of *P. Bakeri*.

11. *PHACELIA CONGESTA* Hook., Bot. Mag. LXII: t.3452 (1835).

Erect annual or biennial 2-5 dm. high; stem simple or diffuse, branching from base; herbage viscid-glandular, often silvery-pilose; leaves ovate, once or twice pinnatifid, the three terminal lobes usually larger, lobes or pinnae sharply cut; inflorescence paniculate or cymose; scorpioid racemes 3-5 mm. long often lengthening considerably in age; pedicels 1-3 mm. long, elongating in fruit; calyx-lobes 3-4 mm. long, narrowly lanceolate, oblanceolate or linear, one-half to two-thirds as long as corolla, and from just slightly longer than capsule to twice as long; corolla blue, campanulate, 5-7 mm. long, 3-6 mm. wide, appendages in corolla broadly lunate, attached less than 0.5 mm. from base of corolla, stamens and style usually exerted about 2 or 3 mm.; seeds 2.25-2.7 mm. long, 1.3 mm. wide, foveolate, the ventral surface excavated on each side of salient ridge.

KEY TO VARIETIES OF *PHACELIA CONGESTA*

Capsule with 2 seeds. Vicinity of Dallas, Texas.....11a. var. *dissecta*  
Capsule with 4 seeds.

Plant grayish pubescent. From western Texas, New Mexico, and adjacent Mexico.....

.....11b. var. *rupestris*  
Plant green. From central Texas, northeastern Mexico, eastward.....11c. var. *typica*

11a. *PHACELIA CONGESTA* Hook. var. *DISSECTA* Gray, Syn. Fl. II: 1: Suppl., 415. 1886.

Plant 3-5 dm. high; stem simple, finely pubescent above, becoming nearly glabrous below; leaves 3-10 cm. long, 3-4 cm. broad, alternate or opposite, mostly in upper part of plant, finely pinnate into numerous lobes, hispidulous and glandular on both sides, grayish or silvery beneath, greener above; corolla 7 mm. long, 5 mm. wide; stamens irregular in length, sometimes equaling corolla, more often exerted to not more than 2 mm.; seeds 1 or 2, 2.25 mm. long, 1.25 mm. wide.

Type locality, Dallas, Texas. Specimens seen: shaded rocks, Dallas, Texas, *Reverchon, May & July* (G, N); Dallas, Texas, rocky woods, *Reverchon, May 1880* (G).

(to be concluded)

## The part played by auxin in the formation of internal intumescences in the tunnels of leaf miners<sup>1</sup>

CARL D. LA RUE

(WITH ONE FIGURE)

During several summer seasons the author has examined the tunnels of leaf miners, and has noted that although the tunnels are usually not filled in by any cell outgrowth, in some cases masses of cells fill them partially or completely. In several species the outgrowths were seen along the course of the larger veins, but in others the masses of tissue were formed wherever the feces of the larvae had been deposited in contact with the mesophyll of the leaf. In thinking over these observations and correlating them with recent results in the study of the growth hormone, the writer came to the conclusion that there was a definite connection between these cell outgrowths and the presence of auxin, the plant growth hormone. Since auxin had been shown to be present in the urine and feces of numerous animals it appeared likely that auxin would be present in the feces of insect larvae. It appeared that if the feces of insect larvae contained auxin, then a possible explanation of the outgrowth of cells in the tunnels of insect larvae in leaves would be at hand.

Later the author (La Rue 1936, 1937) found that intumescences on poplar leaves could be produced by applications of auxin and heteroauxin, and that cell outgrowths similar to those found in the tunnels of leaf miners could be induced by applications of hetero-auxin to the exposed mesophyll of leaves of *Mitchella repens* and *Coreopsis lanceolata*.

Still later it was found that Küster (1911) had figured cell outgrowths in an insect gall where the feces of the insect larva were in contact with the cells of the host plant. Küster assumed that some chemical stimulus was absorbed from the feces by the plant cells and that this caused the cell outgrowth.

Erwin Smith (1920) in his book on Bacterial Diseases of Plants has given a rather extensive discussion of abnormal growths in which, as is well known, he was intensely interested. He observed that insects which lived with the mouth parts, whole head or fore part of the body buried in plant tissue never formed galls, but that the gall-forming larvae were always completely surrounded by plant tissue, from which facts he assumed that the excretions or secretions of the posterior end of the larvae might act as a stimulus to gall formation.

<sup>1</sup> Papers from the Department of Botany, University of Michigan no. 587, reporting work done at the University of Michigan Biological Station.

The structures in question here are of themselves of minor importance but as the beginning of an insight into the problem of gall formation in general they may be of considerable significance.

#### OBSERVATIONS

Many mines of insect larvae were found in which no cell outgrowths occur. As is well known many leaf-mining larvae dispose of their frass in networks of silk suspended in the tunnels in such a way as not to come into contact with the plant cells. Other species deposit the feces over the inner surface of the epidermis, and in but one instance have these been seen to stimulate any growth of the epidermal cells. That was in *Aquilegia canadensis*. Anthocyanin often developed in epidermal cells in

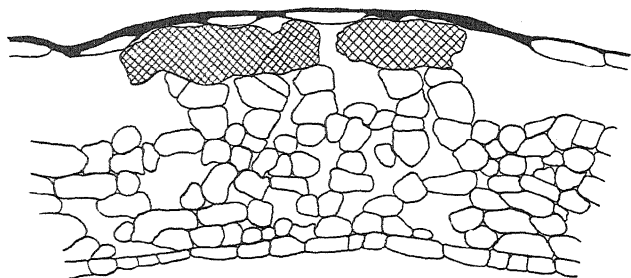


Fig. 1. Cross section of a leaf of *Nemopanthus mucronata* cut through a tunnel made by a leaf-mining insect. The insect has removed the palisade parenchyma. The pellets of feces are cross-hatched. They were deposited on the spongy mesophyll and have been pushed upward against the epidermis by the growth of the mesophyll cells.

contact with feces. Some species smear the feces rather generally over the inside of the tunnel and in these cases it was usually impossible to be sure that there was any stimulus to growth of the cells.

In the tunnels where the feces were found in direct contact with the mesophyll cells of the leaves cell outgrowths were not always induced. Examples of such species were the mines in leaves of *Pteris aquilina*, *Smilacina racemosa*, *Ulmus americana*, *Aralia nudicaulis* and *Aster macrophyllus*, although the last named species had outgrowths along the larger veins. A direct relation between contact of the feces with mesophyll cells and the outgrowth of the cells was found in *Diervilla lonicera*, *Aquilegia canadensis*, *Solidago* sp., *Aster laevis*, *Oenothera biennis*, *Quercus borealis* and *Nemopanthus mucronata*.

Leaves of *Aster laevis*, *Solidago* sp., and *Nemopanthus mucronata* containing mines were imbedded in paraffin and sectioned. The sketch in figure 1 gives a fair representation of one of the smaller outgrowths in relation to the pellet of feces.

In general the outgrowths consist merely of enlarged cells which have stretched far beyond their normal dimensions. In some examples cell division also seems to have taken place. The masses bear a very strong resemblance to the intumescences reported by several authors on a number of species and studied in some detail by the writer (1933b, 1933c) in *Populus grandidentata* and *P. tremuloides*. If they appeared on the surfaces of the leaves they would without doubt be called intumescences, so for purposes of classification they will be designated here as *internal intumescences*, although Sorauer (1909) used the term in a somewhat different sense.

#### EXPERIMENTAL STUDIES

In a paper on the water supply of the epidermis of leaves the author (1930) has described the separation of the lower epidermis and a hypodermal layer from the mesophyll in leaves of *Mitchella repens*. Since these layers are normally separated from the mesophyll and can be removed without injury to that tissue this species suggested itself as one well suited to attempts to cause cell outgrowths by the application of feces of insects and other animals to the leaf tissues.

##### *Application of feces.*

*Experiment 1.* The lower epidermis was removed from leaves of *Mitchella repens* and the leaves were laid in moist chambers with the upper epidermis in contact with moist filter paper, or paper toweling. On the exposed mesophyll of each experimental leaf two pellets of feces of the mouse were laid. A number of leaves with exposed mesophyll were left without pellets as controls. *Results.* An area under each pellet showed discoloration and many cells were dead in this area. But just beyond the injured area, which was circular in shape, a dense rampart of cell outgrowths appeared. Beyond this ring of outgrowths occasional cells showed growth. The margins of the leaves where the lower epidermis had been torn away showed extensive outgrowths. The control leaves showed some scattered small outgrowths. In spots where cells had been crushed in removing the epidermis, outgrowths were numerous but small. In another paper (La Rue, 1937) the author has shown figures of normal leaves of this species, as well as of control leaves with small outgrowths.

*Experiment 2.* As for Experiment 1 except that several pellets of feces from leaves of *Populus grandidentata* which had been rolled up by a leaf-roller were used. *Results.* The toxic areas were smaller than those in Experiment 1, probably because the pellets were smaller. A very heavy border of cell outgrowths was formed around each pellet. Control leaves appeared as in Experiment 1.



*Experiment 3.* As for Experiment 1 except pellets from an insect larva living on peach leaves were used. *Results.* Exactly as in Experiment 2.

*Experiment 4.* As for Experiment 1 but pellets from sawfly larvae on tamarack were applied. *Results.* As in Experiments 2 and 3.

*Experiment 5.* As for Experiment 1 except that feces from tent caterpillars on walnut trees were applied. *Results.* As in Experiments 2, 3, and 4.

*Experiment 6.* As for Experiment 1 but very tiny pellets were transferred from tunnels in goldenrod leaves to the mesophyll of leaves of *Mitchella repens*. *Results.* Under each pellet a crater-like mass of cells was formed with the pellet lifted up slightly and held in the center of the mass. This was identical in appearance with some of the outgrowths actually seen in tunnels formed by larvae of leaf-miners. Control leaves appeared as in Experiment 1.

*Experiment 7.* Leaves of *Aquilegia canadensis* with leaf-miner tunnels in them were taken. The tunnels were opened exposing the mesophyll and the leaves laid, mesophyll up, on moist paper toweling in a damp chamber. Pellets from insect larvae feeding on maple leaves were applied to the mesophyll. *Results.* Leaves yellowed and became rather dry. No outgrowths were produced.

*Experiment 8.* Lower epidermis was peeled from the leaves of *Aster laevis*. Pieces of leaves were put in a damp chamber with the upper surface in contact with moist paper toweling. Pellets from a poplar leaf-roller were laid on the exposed mesophyll. Pieces of leaves with exposed mesophyll but without feces kept as controls. *Results.* Areas under and around the pellets were discolored and in some pieces dead, but beyond these areas cell outgrowths arose from the mesophyll. Cell outgrowths were numerous along the cut edges of the experimental and control pieces alike, but the mesophyll of the control pieces showed few and scattered outgrowths.

#### DISCUSSION

From the observations recorded it is apparent that the feces of leaf-mining larvae in leaves are able to cause cell outgrowths when they come into contact with the cells along the walls and bottoms of the tunnels. The observation is shown to be correct by the induction of outgrowths, or internal intumescences, by the application to mesophyll cells of the feces of some six species of leaf-mining larvae. Although no proof was secured of the presence of auxin in these feces, and in those of mice which were used successfully also, their effect strongly suggests the presence of the plant growth hormone. That auxin has been found in the feces of other animals

is another indication. The fact that the author has produced similar structures on leaves of *Mitchella repens* (La Rue, 1937) and intumescences on leaves of *Populus grandidentata* (La Rue 1936) by applications of hetero-auxin makes the assumption that the auxin in the feces is responsible for these internal intumescences still more reasonable.

The outgrowths often seen in tunnels of leaf-miners where the tunnels have crossed veins of good size or run alongside them may be explained on the same basis as the formation of callus at the lower ends of cut veins as reported by the writer (1933a) in his work on regeneration of leaves and cotyledons. Avery (1935) has shown that auxin is accumulated in and transported through the veins of tobacco leaves, and that it is more abundant there than in the other cells of the leaf. In these tunnels and at the cut ends of veins cell outgrowths are doubtless caused by the presence of auxin in the phloem. The author has observed this outgrowth along veins exposed by wounding in a number of species.

There is very great variation in the ability of cells of various tissues in different species to react to wounding when the wounded surfaces are kept from drying by a moist atmosphere, exactly the condition found in tunnels of leaf-miners. Some plants always produce masses of growth from cortex, pith, cambium, and vascular rays. In other species the possibility of outgrowth is localized while in some it scarcely exists at all. Such a leaf as that of *Mitchella repens* is excellent material for the purpose for which it was used in this study because it usually forms only scattered outgrowths except along main veins, and in areas where cells have been crushed, but occasionally it produces more extensive intumescences (La Rue, 1933c). The details of cell reaction of wounded surfaces in damp atmospheres have been given in another paper (La Rue, 1937), but the author feels that he understands the nature of such reactions well enough to hazard the suggestion that auxin was the active agent in inducing the outgrowths described here, and that the very sporadic and limited outgrowths produced on the mesophyll of the control leaves were limited because of the limited supply of auxin in the mesophyll of those leaves.

The relation of the growths described in this study to true galls is naturally vague as yet. It does appear, however, that the plant growth hormone must play an important part in the growth of galls, especially those which represent hypertrophy. Hyperplasias may not be related to the growth hormone, though we are yet very uncertain as to the effect of auxin on cell division. The question of the differentiation of gall tissues does not seem to be connected with the action of the growth hormone though even this possibility is not excluded. The author feels that this small study is an opening wedge into the investigation of the hormone relations of plant

galls, a study which he believes will be fruitful and one which he hopes to pursue in the future.

#### SUMMARY

1. In most tunnels eaten out of leaf tissue by the larvae no outgrowth of the bordering cells takes place. In others masses of cells develop from exposed veins, and in a third group, masses of cells are produced by the mesophyll cells with which feces of the larvae have come into contact.

2. The outgrowths usually consist of cells swollen much beyond their original dimensions but in others cell division also occurs.

3. The outgrowths bear strong resemblances to the intumescences often developed on the surfaces of leaves and stems and are designated here as *internal intumescences*.

4. Pellets of feces of a number of insect larvae, and of mice, induced the formation of cell outgrowths on the exposed mesophyll of leaves of *Mitchella repens* and of *Aster laevis*.

5. This study is the beginning of the investigation of the hormone relations of plant galls.

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A New England station for *Laminaria faeroensis*  
Børg; forma

DUNCAN S. JOHNSON

During summers from 1922 to 1926 spent at the Mt. Desert Biological Laboratory at Salsbury Cove, Maine, the writer collected at Sullivan River Falls, Frenchman's Bay, Maine, several species of *Laminaria*. Among them was one that was at first regarded as *L. longicuris*. When, however, this alga was again collected in August, 1927, during a visit to the laboratory of Dr. Kathleen M. Drew of Manchester, England, her familiarity with the kelps of both Europe and America enabled her to recognize the Sullivan Falls kelp as distinct from the usual types of *L. longicuris* De La Pyl. Dr. Drew took specimens of the plant to England, and after comparing them with plants in herbaria there, found them most like *Laminaria faeroensis* Børg. She therefore sent them to Prof. F. C. E. Børgesen at Copenhagen, who identified the plant as close to *Laminaria faeroensis* Børg. Specimens of the same plant collected by the writer on September 1, 1928, and others collected by W. R. Hatch on July 3, 1933, have been studied by Prof. Wm. R. Taylor of the University of Michigan, and will be briefly characterized by him in a forthcoming book on marine algae.

This species of *Laminaria* has not been recognized on collecting trips to other shores of Frenchman's Bay, of Mt. Desert Island, and of Schoodic Point. This note is published in the hope that algologists in New England will be on the look-out for this plant elsewhere. It is conceivable that this *L. faeroensis* is a recent immigrant to our shores that has found a suitable habitat in this three-foot tidal fall where the water is almost constantly flowing rapidly but is never subjected to violent wave action. If it is such an immigrant, it will be interesting to watch for its spread to other suitable habitats on the New England coast. This, it will be recalled, was the manner of occupation of that coast by *Dumontia incrassata* (O. F. Mueller) Lamaroux, which was first found on our Atlantic coast, by the writer and Grace A. Dunn, at South Harpswell, Maine, in June, 1913. This species was then evidently a very recent immigrant, for it had not been seen there by the veteran algologist F. S. Collins, who had carefully studied the algal flora there only a year or two before. This alga has since been reported, I believe, from a number of points on the New England coast, as far south as Rhode Island (W. A. Setchell, *Rhodora* 25: 33-77. 1923), and also from Nova Scotia.

THE JOHNS HOPKINS UNIVERSITY  
BALTIMORE, MARYLAND

# INDEX TO AMERICAN BOTANICAL LITERATURE

## 1931-1936

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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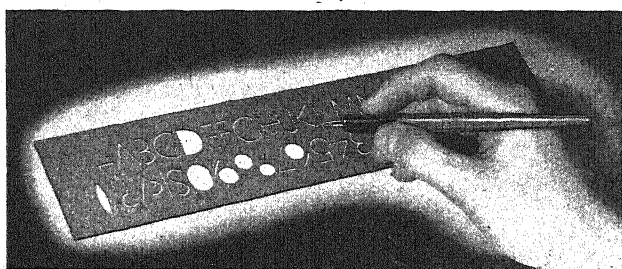
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## Flue-cured tobacco: a comparative study of structural responses induced by topping and suckering

FREDERICK A. WOLF AND P. M. GROSS

(WITH FOURTEEN FIGURES)

Investigations involving flue-cured tobacco have been in progress for several years in the laboratories of Duke University. Results which deal with the influence of weather upon type and quality, with the chemical changes that occur during natural aging, and with the correlation of the chemical composition of cured leaves with their position on the stalk, have already been published (Darkis *et al.*, 1935, 1936). Certain other portions of these investigations are not yet completed. The present report deals with a study of structural modifications that occur in flue-cured tobacco following the removal both of the flowering stalk, a practice called topping, and of the axillary buds, a practice called suckering. The findings relating to the physical and chemical changes induced by these practices are reserved for presentation in a subsequent report.

Several investigators have recently given consideration to the morphological effect of topping and suckering of tobacco. The present status of this problem together with their own experimentation is summarized in the publications of Berthold (1929, 1931) and Avery (1934). None has dealt with flue-cured tobacco except Avery whose findings are based upon results with potted plants. Our results with field-grown plants differ from those of these recent investigators mainly in degree rather than in kind. They are therefore, largely confirmatory but are believed to contribute additional features of interest and value.

### MATERIALS AND METHODS

Plants of *Nicotiana Tabacum* L. of the variety Cash were used in this study. They were grown in plots, during the summer of 1935, at the Tobacco Experiment Station, Oxford, N. C. Equal amounts of commercial fertilizer were applied to each of three plots immediately prior to transplanting. The seedlings were transplanted on May 17. The two lowermost leaves were removed from all of the plants on July 12. On this date the plants were of sufficient size to permit the removal of the tops and to allow nine leaves to remain on each stalk. Accordingly, on July 12, all plants in one plot were topped to a height of nine leaves. These plants are regarded as "low-topped," and are representative of the topping practice used by growers who harvest the crop by cutting the entire stalk rather than by priming. By July 20, the plants were of sufficient height to allow eighteen

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leaves to remain after topping. Accordingly the tops were removed from all plants in a second plot, permitting them to bear eighteen leaves. This type of topping is representative of "high-topping," as employed by growers who harvest the crop by priming off the leaves as they mature. All of the suckers were removed one or more times each week from the plants in



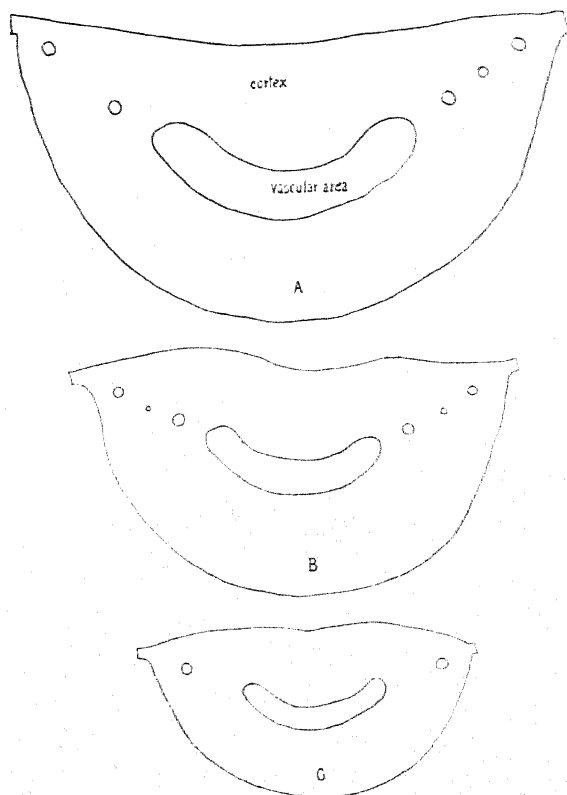
Fig. 1. Sketches of low-topped, high-topped and non-topped tobacco plants as they appeared at the beginning of harvest. (Drawn to scale from photographs.)

these two plots. The plants in the third plot were not topped, consequently no suckers developed, and they bore an average of twenty-three leaves per plant.

The data upon which this report is based are concerned with three selected, representative plants from each of the three plots. The remainder of the plants were used in the studies of modifications in chemical composition caused by topping, to be subsequently reported. The leaves were harvested as they matured, beginning on July 29. In the case of the low-topped plants, harvesting was concluded on August 26, and on August 31

in the case of the high-topped plants. The last leaves were harvested from the non-topped plants on September 10.

Leaf area was determined by tracing the patterns of the leaves, then weighing the paper patterns, and finally computing the leaf areas from the weights of the patterns. The area of the midrib and of its central vascular



Figs. A, B and C. Diagrams showing proportional average size of transectional areas of midribs of low-, high-, and non-topped plants, respectively. The crescentic areas are outlines of the central vascular bundle.

axis, in transection, were determined by cutting free-hand sections of the midrib immediately above the axillary buds and then tracing the midrib area and vascular-axis area. These tracings were made with the magnification of a dissecting microscope and with the aid of a camera lucida. The patterns were afterward weighed and the midrib and vascular axis area, both magnified and actual, were computed.

The positions of the principal veins were indicated when the leaf-area patterns were made. The leaves were first perforated at the juncture of a principal vein with the midrib and then again at a point beside the vein and approximately midway between the midrib and the leaf-margin. The line joining these two points thus marked the position of that vein and the angle which it formed with the midrib.

Leaf thickness was determined with a Randall and Stickney gauge caliper provided with a 13 oz. weight and calibrated in one-thousandth cm. As the result of several series of preliminary measurements it was learned that the tobacco leaf is variable in thickness. One half of the lamina is usually thicker, moreover, than the other. Leaves are found to be thinnest near the base and gradually to increase in thickness toward the tip, but to be slightly less thick at the extreme tip and margin. Furthermore they are thickest near the midrib, slightly less thick along the margin and intermediate in thickness in the area approximately median between the midrib and the leaf-margin. For these reasons from 15 to 25 measurements were made of the thickness of each half of the lamina along the region median between the margin and the midrib. The average of these 30 to 50 measurements was taken as the leaf-thickness. As a check on this method, and in order to secure preparations for comparative cellular measurements, four samples, two from each half of the lamina, were collected. Two of these samples were taken from the median area immediately above the third vein from the base of the leaf, and the other two from immediately below the third vein from the tip. The samples were preserved in formal-acetic-alcohol, and were later embedded in paraffin, sectioned, and stained. Samples of midribs were preserved in the same fixative solution for embedding. The drawings of comparative cellular structure of leaves and of midribs were made with the aid of a microprojector.

#### COMPARATIVE LEAF DIMENSIONS

*Size.* Topping and suckering modify the growth of the entire plant, even of the root system (Berthold, 1931). Growers of tobacco have for a long time known that both the yield and quality of the crop are affected by the removal of the top and axillary buds of the tobacco plant, and that these practices are analogous to pruning as employed by gardeners and orchardists. The most obvious modification however, induced by these practices, involves the size of the leaves. This feature is shown in degree in figure 1, which is drawn to scale from photographs of plants taken at the beginning of harvest. The leaves of these plants, except a few of the lowermost ones on the high-topped plants and the non-topped plants, continued to grow until they were primed. Consequently much greater differences

TABLE 1  
*Leaf dimensions and areas of low-topped plants*

NUMBER OF LEAF	LENGTH (CM.)	WIDTH (CM.)	AREA (SQ. CM.)	LENGTH WIDTH	THICKNESS ( $\mu$ )	TRANSECTION AREA OF MIDRIB (SQ. CM.)	TRANSECTION AREA OF VASCULAR AXIS (SQ. CM.)
1	52.6	29.6	982.68	1.777	359	.633	.063
2	60.2	33.0	1269.27	1.827	351	.823	.076
3	59.1	32.6	1206.10	1.812	306	.813	.087
4	61.8	35.3	1368.40	1.758	294	.953	.108
5	62.3	35.9	1424.56	1.745	299	1.024	.097
6	65.3	36.5	1523.56	1.794	299	1.094	.122
7	68.8	38.3	1628.41	1.803	311	1.157	.143
8	67.0	39.6	1658.36	1.705	301	1.269	.139
9	68.6	42.6	1844.45	1.608	407	1.378	.178
Average	62.85	35.93	1433.97	1.759	325	1.016	.1126

than those noted in figure 1 would have been shown if an ideal sketch had been made displaying the comparative leaf sizes as they were when each leaf was primed.

TABLE 2  
*Leaf dimensions and areas of high-topped plants*

NUMBER OF LEAF	LENGTH (CM.)	WIDTH (CM.)	AREA (SQ. CM.)	LENGTH WIDTH	THICKNESS ( $\mu$ )	TRANSECTION AREA OF MIDRIB (SQ. CM.)	TRANSECTION AREA OF VASCULAR AXIS (SQ. CM.)
1	45.6	25.0	704.19	1.838	347	.455	.0395
2	51.2	27.8	894.62	1.843	345	.530	.0500
3	50.6	27.5	862.96	1.834	325	.589	.0700
4	53.8	27.5	1016.40	1.753	307	.698	.0750
5	54.2	29.0	993.99	1.846	264	.633	.0700
6	59.3	33.5	1204.84	1.772	269	.762	.0827
7	56.0	31.0	1103.88	1.816	242	.746	.0757
8	58.8	31.3	1183.65	1.882	271	.796	.0843
9	58.0	30.8	1152.27	1.887	256	.818	.0813
10	58.6	30.0	1099.77	1.962	242	.735	.0847
11	58.3	30.2	1045.53	1.938	240	.826	.0900
12	54.8	27.8	925.68	1.972	204	.793	.0725
13	58.2	30.3	1074.45	1.926	240	.754	.0887
14	58.3	29.8	1058.66	1.965	251	.777	.0980
15	56.8	28.7	983.54	2.015	295	.640	.0800
16	57.0	30.8	1092.32	1.857	321	.858	.1127
17	53.0	26.5	895.38	2.002	322	.836	.1170
18	52.3	27.0	900.69	1.960	377	.782	.1157
Average	55.27	29.14	1010.71	1.892	284	.724	.0826

Leaves that are most mature at time of topping are least modified, and conversely those that are least mature are most profoundly modified, facts with which every grower is familiar. As might be anticipated, therefore, the largest leaves are produced as the result of low-topping, and the leaves of high-topped plants are larger, on the average, than are those on plants whose tops have not been removed (tables 1, 2, 3). The average leaf-areas of the three plants used in each of these three types of treatment

TABLE 3  
*Leaf dimensions of non-topped plants*

NUMBER OF LEAF	LENGTH (CM.)	WIDTH (CM.)	AREA (SQ. CM.)	LENGTH WIDTH	THICKNESS ( $\mu$ )	TRANSECTION AREA OF MIDRIB (SQ. CM.)	TRANSECTION AREA OF VASCULAR AXIS (SQ. CM.)
1	48.2	26.8	790.95	1.807	344	.570	.0703
2	49.6	28.2	883.13	1.763	326	.619	.0657
3	51.8	29.8	856.45	1.965	292	.569	.0653
4	53.6	27.8	937.57	1.939	298	.599	.0700
5	55.5	30.0	1023.36	1.866	287	.640	.0773
6	57.3	30.3	1075.92	1.909	295	.691	.0897
7	54.3	28.0	947.05	1.948	237	.634	.0820
8	53.2	29.2	1063.07	1.951	270	.738	.0770
9	56.6	28.0	965.13	2.024	244	.727	.0823
10	55.5	27.5	953.42	2.025	224	.690	.0707
11	57.5	26.5	973.54	2.173	233	.658	.0747
12	53.0	26.5	886.47	2.040	256	.714	.0720
13	54.3	27.3	937.52	1.946	260	.734	.0747
14	51.5	26.8	837.27	1.952	221	.624	.0723
15	49.3	24.8	729.70	1.975	177	.592	.0637
16	45.0	22.2	596.82	1.979	180	.492	.0530
17	43.6	19.8	527.27	2.062	186	.446	.0480
18	42.2	17.2	489.03	2.227	240	.371	.0380
19	44.2	23.2	587.35	2.126	277	.403	.0523
20	43.3	20.2	542.54	2.144	271	.379	.0330
21	41.2	19.5	494.98	2.177	300	.376	.0330
22	40.3	19.3	550.54	2.266	311	.407	.0515
23	36.5	16.8	369.69	2.364	302	.282	.0350
age	49.43	25.03	783.42	2.024	262	.563	.0631

are 1433.97, 1010.71, and 783.42 sq. cm. The greater than usual average leaf surface induced by topping thus depends in part upon the height of topping, i.e. upon the number of leaves allowed to remain upon the stalk.

It may be noted, in the case of low-topped plants, that the size of the leaves increases progressively from the base to the tip of the stalk and that even the lowest leaves are larger than those of plants of the other treatments (table 1). Apparently no increase in size is exhibited by the lowermost leaves of high-topped plants, if comparison of their leaves is made

with corresponding ones of plants whose tops have not been removed. The largest leaves of high-topped plants tend to be inserted along the median third of the stalk (table 2), and the leaves of the non-topped plants become progressively smaller from the middle of the stalk toward the tip (table 3). Berthold (1929) summarized his observations on the effect of topping on leaf size by stating that the final size of the leaf is determined by the height of the leaf on the stalk, by cultural practices, by the variety of tobacco, and by the size the leaf had attained when the plant was topped.

From the data in tables 1, 2, and 3, it may be seen that the average area per leaf of a non-topped plant is approximately 54% of that of low-topped ones, and 77% of that of high-topped ones. This increased leaf area is not the result of a proportional increase in length and width. The average length of the leaves of the low-topped, high-topped and non-topped plants is 62.86, 55.27, and 49.43 cm., and their width 35.93, 29.14 and 25.03 cm. respectively (tables 1, 2, and 3). The average proportionality of length and width is therefore, 1.759, 1.892, and 2.024 for these three types of treatments, indicating that the shape of the leaf is most profoundly modified by low-topping. The increased width induced by topping is not a uniform one in all portions of the leaf, but instead it is most pronounced near or above the middle of the leaf. The leaves of topped plants become, in consequence, less taper-pointed. As was concluded by Berthold (1929) the ratio between leaf length and leaf width differs with position of the leaf on the stalk. Relatively broadest leaves are borne near the top of the stalk on low-topped plants, near the middle in high-topped ones, and below the middle in non-topped ones.

Avery (1933) found that there is a greater growth in one dimension than in the other in certain portions of the leaf, a phenomenon that determines the final shape of the leaf. This fact was learned by dividing the developing leaf into marked segments of uniform area and then making a series of measurements of these areas at proper time intervals. This procedure showed that segments situated along the leaf-margin increase in width more rapidly than those near the midrib. Botanists are without a satisfactory explanation to account for the constancy in shape of the leaves of a particular species of plants, or, for that matter, of the plant as a whole. Growth controlling factors or mechanisms have, of course, been postulated. The fact remains that all further increase in height of the tobacco stalk ceases following the removal of the top, and that the topped plant continues its efforts to establish a new apex. The uppermost axillary buds are the first to develop into shoots to replace the excised top. When these buds are, in turn, removed those in the axils immediately below develop, showing the plant's continuous attempts at expression of "apical-



ness." Another adjustment response to topping which may be termed a compensatory response, is the tendency of topped plants to produce a total green weight of leaves equal to that of non-topped ones, and in so doing the length-width ratio of leaves is disturbed. Might it be that the factors governing "apicalness" in topped plants are less in amount, as the result of topping and suckering, and that the length-width component of

TABLE 4

*Weights of stalks and leaves, and ratio of leaf area to transectional area of the midrib of low-topped, high-topped, and non-topped tobacco plants*

	KINDS OF PLANTS		
	LOW-TOPPED	HIGH-TOPPED	NON-TOPPED
Av. green weight, stalks (gms.)	229.1	515.0	680.6
Av. dry weight, stalks (gms.)	41.4	97.5	138.5
Dry weight, stalks (%)	18.07	18.93	20.20
Av. total green weight leaves per plant (gms.)	715.87	854.70	735.95
Av. total dry weight leaves per plant (gms.)	91.444	113.707	98.25
$\frac{\text{Green Weight}}{\text{Dry Weight}}$ leaves	7.828:1	7.516:1	7.49:1
Av. green weight of leaves (gms.)	79.54	47.48	35.04
Av. dry weight of leaves (gms.)	10.271	6.753	4.373
Dry weight of leaves (%)	12.78	14.22	12.19
$\frac{\text{Midrib Area}}{\text{Vascular Area}}$	9.28	9.01	9.05
$\frac{\text{Leaf Area}}{\text{Midrib Area}}$	1413.3	1396.0	1391.3
Av. volume of leaves	46.60	28.70	20.52

forces within the leaf, postulated in a succeeding paragraph, is overbalanced in favor of the force that controls leaf width?

*Angles of veins.* Apparently the disproportionate increase of width over length of leaves in topped plants, as reflected by greatest differential length-width changes in the median marginal segments, is also indicated by the sizes of the angles made by the principal veins with the midrib. These differences in sizes of angles formed by the principal veins and the midrib, as induced by topping practices, are shown by the data in table 5. The significance of these differences can best be understood if certain facts regarding the development of the tobacco leaf are recalled. By the time that the tobacco leaf has attained one-sixth to one-fifth its mature size, as shown by

Avery (1933), it contains virtually its full complement of cells. At this stage of development the size of the angles of the principal veins of any given tobacco leaf are the same as those of any other leaf of the same stage of development on any other tobacco plant. It seems reasonable to assume, therefore, that the ultimate form of the mature leaf must be the resultant of two growth-force components, one of which operates in a direction parallel to the midrib and the other one at right angles to the midrib, hence abaxial to it. The diagonal of these two forces might be expected, therefore, to be indicated by the ultimate position of the principal veins, with the midrib as the base line. Any disturbance of balance between these two forces, as results when the top of the tobacco plant is excised, would consequently modify the length-width growth ratio of all immature leaves,

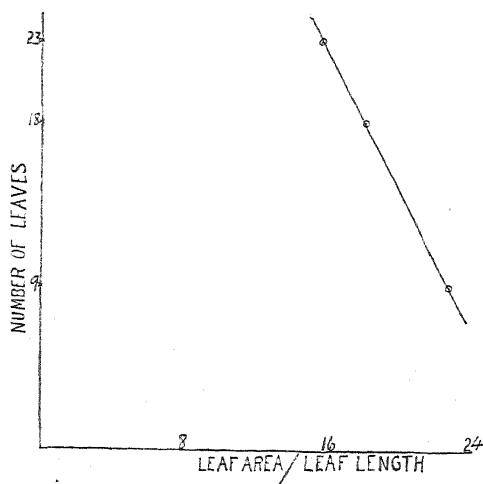
TABLE 5  
*Average size of angle, in degrees, made by pairs of veins and midribs of tobacco*

PAIRS OF VEINS	KINDS OF PLANTS		
	LOW-TOPPED	HIGH-TOPPED	NON-TOPPED
1st	74.1	71.5	67.5
2nd	72.9	69.4	67.5
3rd	68.6	66.5	64.2
4th	63.4	62.0	61.1
5th	59.0	57.8	55.3
6th	53.9	54.4	52.0
7th	49.2	50.0	49.2
8th	46.8	46.6	43.7
9th	43.0	43.0	39.9

and hence the sizes of the angles of the veins. In support of this theory, it may be observed (table 5) that the angles of the corresponding veins are largest in leaves of low-topped plants, smallest in non-topped ones, and intermediate in high-topped ones. These angles, in degrees, for the second pair of veins, for example, are 72.9, 67.5 and 69.4 respectively, for these types of treatments. These differences are not observed in the veins of the upper portion of the leaf to any marked extent, but only in those portions extending up to and including the fifth veins.

It may be pointed out that criteria other than the angles formed by the principal veins with the midrib may be regarded as a measure of the compensatory response of the tobacco plant in manifesting its axial as opposed to its abaxial growth reactions. The existence of this type of response is also shown by the comparison of the average length-width ratios of leaves produced as a result of topping, as previously indicated. Both of these criteria, however, apply to the axial-abaxial growth of the leaf as a unit

rather than to the plant as a whole. Apparently the best conception of the response of the tobacco plant to these opposing growth forces is gained if one considers the length of the stalk as measured by the number of leaves as the axial growth response of the plant. While the lengths of the midribs of leaves represent a type of growth very similar to that of the stalk and should therefore be regarded as axial, differences in midrib lengths may be eliminated and a measure of abaxial growth arrived at if comparison is made of the areas of leaves per unit midrib length. Thus in comparing two

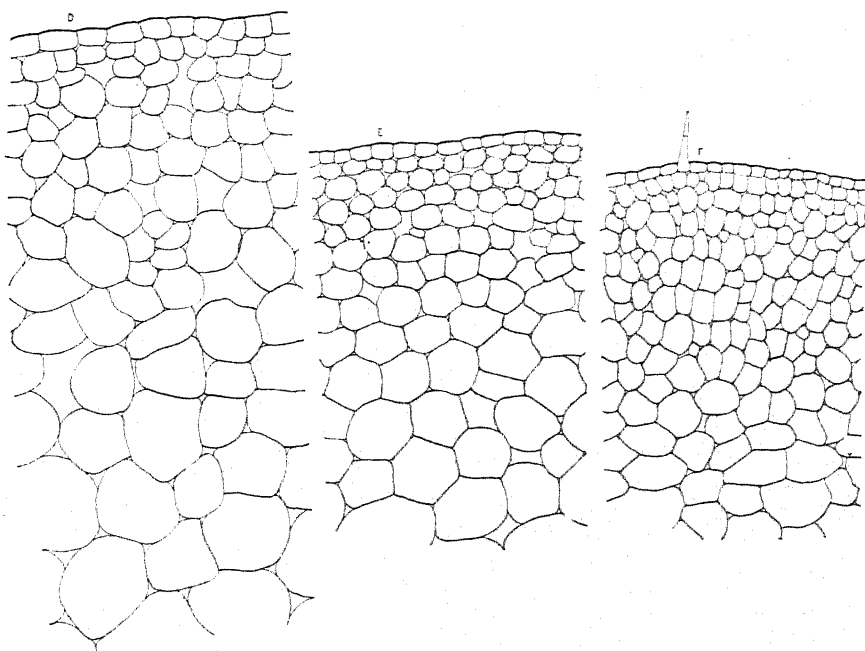


Graph 1. An expression of relationship of axial-abaxial growth forces as modified by topping.

leaves, the one which has the greater area of laminar tissue has, on the average, the greater abaxial growth. On the basis of these conceptions, if a conservational or compensatory mechanism is operative in the tobacco plant it would be anticipated that restriction of the axial growth should result in an increased abaxial growth. In applying this measure of axial-abaxial growth to the present cases the following average leaf areas per unit leaf length are found: for the 9-leaved plants 22.8 sq. cm. per unit length; for the 18-leaved plants 18.1 sq. cm. per unit length; and for the 23-leaved plants 15.8 sq. cm. per unit length. These relationships are portrayed in graph 1 in which the ordinate represents the axial growth (measured by the number of leaves per plant) and the abscissa, the abaxial growth (ratio of average leaf area to leaf length). These data show, in a striking manner, a linear inverse correlation between these two growth forces in the tobacco plant as a whole. Compensatory axial-abaxial growth forces doubtless determine the growth form, i.e. the shape of all other species of plants but their existence could be expected to be more difficult of demonstration than with the tobacco plant.

*Thickness.* As regards thickness of the leaves as affected by topping, it is generally held that the fewer the leaves on the plant the thicker the leaves. This conclusion is supported by the fact that the thickness of the leaves of low-topped plants, taken collectively, is  $325\mu$ , of the high-topped ones,  $284\mu$ , and of the non-topped ones  $262\mu$  (tables 1, 2 and 3). This

increased thickness, induced by topping, is not the result of the formation of new cells, there being no meristematic tissue in the differentiated leaves except in the vascular portion, but to an increase in size of cells. Comparative measurements show that all the cells of the epidermis, palisade parenchyma, and spongy parenchyma are involved (figs. J, K, and L). These results, based upon data from averages of several thousand measurements,

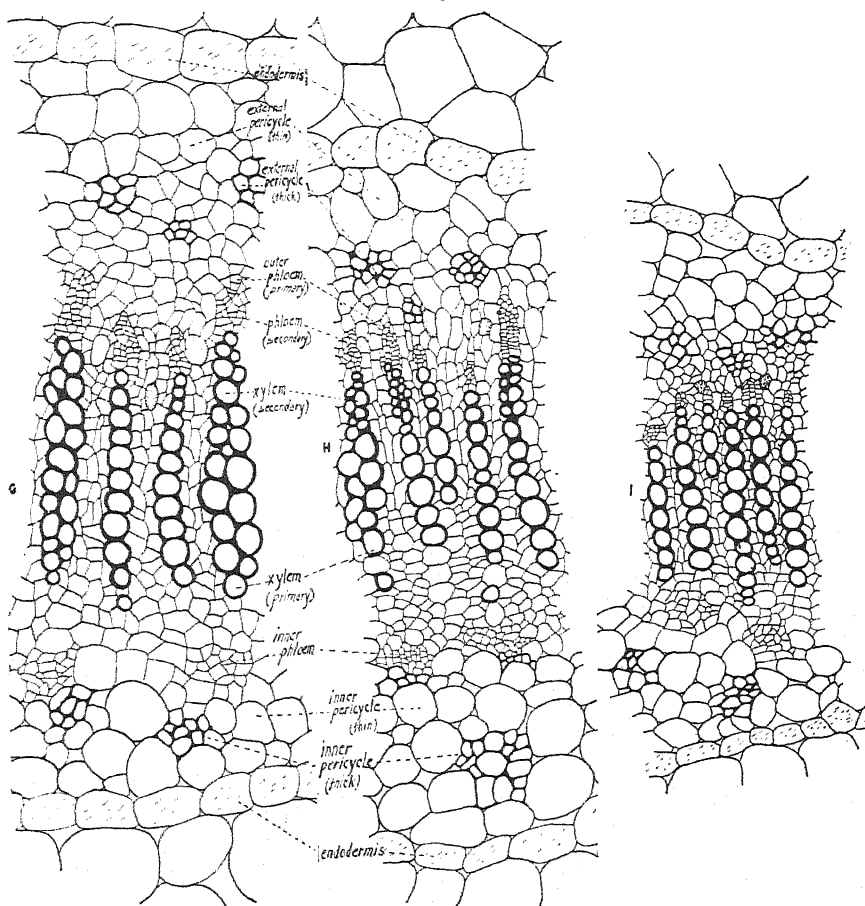


Figs. D, E and F. The proportional size of cortical cells of the midribs of tobacco leaves, D, low-topped, E, high-topped and F, non-topped. Sections show cells to a depth of approximately half the distance from the periphery to the vascular strand.

the details of which are not included, support those obtained by Avery (1934).

Increased thickness coupled with increased leaf area, results in largest volume per leaf of green leaf-tissue, in the case of low-topped plants (table 4). The total green weight of leaves produced by low-topped plants, however, is less than that of the two other treatments (table 4). It may be noted that the largest yield per plant, both in green weight and dry weight of leaves, occurred as a response to high topping. The dry weight of leaves per plant produced by the low-topped plants is approximately 20% less than that of the high-topped ones, and the non-topped plants produced approximately 14% less than the high-topped ones. These results are in general agreement with those obtained by Berthold (1929) who found that

largest yields are secured when plants are topped following the opening of the first flower, and with those of experienced growers of flue-cured tobacco. The disproportion in weight of stalks resulting from these topping

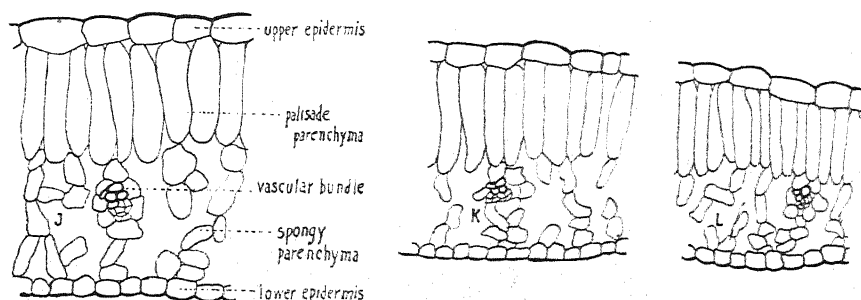


Figs. G, H and I. Transactions of portions of the vascular bundles of midribs of leaves of low-, high-, and non-topped plants respectively. Difference in size of the bundles is due to differences in size of the cells and increased amount of secondary phloem and xylem formed in response to topping.

practices is much greater than that of the leaves as shown by the average green weight per stalk of 229.1, 515.0, and 680.6 grams for the low-topped, high-topped and non-topped stalks, respectively (table 4). A correlation between weight of stalks and weight of leaves, if any exists, is permanently nullified by topping.

## COMPARATIVE MIDRIB DIMENSIONS

The diagrams in figures A, B and C, show the average comparative sizes, in transection, of the midribs of the non-topped and the two types of topped plants. The average transectional area of the midribs of the 27 leaves from the three low-topped plants is 1.016 sq. cm., of the 54 leaves from the three high-topped ones is 0.724 sq. cm., and of the 69 leaves from the three non-topped plants is 0.563 sq. cm. (tables 1, 2, 3); and for the vascular bundles the measurements are .1126, .0826, and .0631 sq. cm., respectively. The ratios of midrib area and vascular area in transection (table 4) are, therefore, 9.28:1, 9.01:1, and 9.05:1, respectively. The agreement in these proportions is remarkably close in view of the small number



Figs. J, K and L. Transections of leaves of tobacco showing relative sizes of the cells of the epidermis, palisade and spongy parenchyma, when the plants are low-topped, J; high-topped, K; and non-topped, L.

of measurements involved, and of the inexactness inherent in the method employed in making the measurements. The conclusion seems justified, as noted by Avery (1934), that a rather constant proportion is maintained between the size of the midrib and that of its vascular axis.

The ratio between leaf area and the transectional area of the midrib is also rather constant. The average ratio of leaf area to midrib area of all leaves on three low-topped plants is 1413.3:1, on the three high-topped plants 1396.0:1, and on the three non-topped plants 1391.5:1 (table 4), from which it is concluded that the trend of leaf area and midrib area to maintain this proportion is not disturbed by topping. The maintenance of this ratio does not involve the production of a larger number of cortical and epidermal cells in the larger midribs. Counts of cell numbers in a line from the periphery to the vascular axis in corresponding areas discloses that the number of parenchymatous cells is approximately the same in all midribs regardless of the topping practice. The cells of the epidermal and cortical tissues are largest in the largest midribs, figs. D, E, F. Two factors

are operative, however, in the increased size of the vascular axis of topped plants. One of these is the increase in size of the cells of the fundamental tissue. The other is the stimulation of meristematic activity as a result of which more secondary lignified xylem elements occur in the larger midribs and more secondary cells occur in the external phloem. There does not appear to be any change in the number of cells in the internal phloem. These comparative cellular conditions in the midribs of leaves of low-topped, high-topped and non-topped plants are portrayed in figs. G, H, and I. Each section represents a strip of vascular tissues from the dorsal to the ventral side of the axis.

#### SUMMARY

Removal of the flower stalk and axillary buds of tobacco results in an increase in size of the leaves. The size and age of the leaves at the time these operations are performed are prominent factors in determining the amount of this increase. Greatest increase in leaf size occurs in low-topped plants whose suckers are removed at frequent intervals. Greatest total increase in leaf area and greatest weight of leaves per plant result from high-topping.

The increase in laminar size following topping tends to be proportional to the increase in transectional area of the midrib which is in turn proportionally correlated with the transectional area of the central vascular axis.

The greater than usual increase in size of the parenchymatous laminar portions of the leaf, after topping, is due to a greater than usual increase in cell size, all tissues, epidermal, palisade parenchyma and spongy parenchyma, being involved. Cambial activity accounts for additional vascular tissue. Large mature leaves therefore, tend to be composed of the same number of non-conducting or parenchymatous cells as small mature leaves.

Differences in length-width ratios of leaves, a response to topping, is postulated to be due to a disturbance of balance of growth forces that control length and width of leaves. The angles of the principal veins are believed to indicate the component of these two forces. A linear inverse correlation exists between the number of leaves on the stalk (height of topping) and the ratio of leaf area to leaf length.

Topping and suckering stimulate increase in leaf thickness. Average leaf thickness is greatest in low-topped plants.

The increase in size of the petiolar area in topped plants is due to an increase in cell size of all parenchymatous tissues coupled with the laying down of secondary phloem and secondary xylem. The amount of secondary

phloem laid down is meagre in comparison with the amount of secondary xylem.

The average dry weight of leaves produced per plant, i.e. yield, is greatest when plants are topped high, and that of the stalks is greatest in plants that are not topped.

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## A revision of the *Phacelia crenulata* group for North America

JOHN W. VOSS

(concluded)

11b. *PHACELIA CONGESTA* Hook. var. *RUPESTRIS* (Greene) Macbride, Cont. Gray Herb. 49: 25 (1917).

*P. rupestris* Greene Leaflets 1: 152. 1905.

Herbage pilose with silvery hair; corollas usually about 5 mm. long, 4 mm. wide.

Type locality, 1 mile west of Hillsboro, Sierra County, New Mexico. Ranging from southwestern Texas, New Mexico and southeastern Arizona southward to central Mexico. Representative specimens: UNITED STATES, NEW MEXICO: 1 mile west of Hillsboro, Sierra County, *Metcalf* 1012, type (G, P, N); Gila Hot Springs, Mogollon Mts., Socorro County, *Metcalf* 829 (N, P, G, C), *Wright* 1574 (G, N), 1575 (G, N), 1576 (G, N); Organ Mts., Dona Ana County, *Wootton* 135 (C, G, N, P); Carlsbad, A. *Nelson* 11384 (C); Pyramid Peak, Dona Ana County, *Fosberg* S3226 (C, P); Florita Mts., *Jones* on Sept. 7, 1903 (P). ARIZONA: Chiricahua Mts., *Goodding* 2330 (C). TEXAS: Davis Mts., Jeff Davis County, *Moore and Steyermark* 3100 (C, G, N); Limpia Canyon, Davis Mts., *Hanson* 747 (G); Chisos Mts., Brewster County, *Moore & Steyermark* 3325 (C, G, N); Bexar County, *Jermey* in 1904 (N); Kinney County, *Cory* 628 (G); Sheffield, *Jones* 28498 (C). CHIHUAHUA: Santa Eulalia Mts., *Pringle* 364 (C, G), and 162 (G); Colonia Juraz, Sierra Madre Mts., *Jones* on Sept. 2, 1903 (P). COAHUILA: 6 miles east of Saltillo, *Palmer* 850 (G).

In this variety there is considerable intergradation with var. *typica* in the material from southern and western Texas. However, in New Mexico and Arizona the characteristic indumentum of var. *rupestris* makes it easily distinguishable.

11c. *Phacelia congesta* Hook. var. *typica* Voss. n. nom.

*P. congesta* Hook, l.c. *P. conferta*, G. Don. Gen. Syst. Gard. 4: 397. 1837.

Stem and leaves sometimes glabrous, and often covered with a fine puberulence; corollas usually about 5 mm. long and 5-6 mm. wide.

Type, from Texas, *Drummond* 303. Range, northeastern Mexico, Texas and eastward. Specimens seen; UNITED STATES, TEXAS: *Drummond* 303 type collection (G); San Diego, *Croft* 12 (N); San Marcos and vicinity, *Stanfield* in 1897 (N); Nueces Bay, *Heller* 1432 (C, G, N); Austin, *Hall* 474 (N); Laredo, *Reverchon* 3888 (G, P, N); San Angelo, *Reverchon* 3889 (N); near Mathis, San Patricio County, *McKelvey* 1716 (P); Roosevelt, *Jones*

28499 (C, P); Sonora, *Jones 25749* (P); Bellavaco, *Delacour in 1841* (P); San Antonio, *Thurber in 1853* (G, N); west of Uvalde, *Jones 28501* (P); Corpus Christi, *Tracy 9192* (G, N); MEXICO: Monterey, *Canby 166* (G); Monterey, *Palmer 2028* (G); Rio Grande Valley near Diaz, *Pringle 9013* (G).

This plant seems to adapt itself well to various localities and has been cultivated in the Eastern United States and Europe.

12. *PHACELIA SPLENDENS* Eastwood, *Zoe* 4: 9. 1893.

*P. glandulosa* subsp. *splendens* (Eastwood) Brand, *Pflanzenreich* IV, 251: 83. 1913.

Annual, 1–3 dm. high, erect; stems branching from base or simple, often striate, reddish and occasionally yellowish in color, usually glabrous, seldom glandular or glandular pubescent; leaves ovate, 1.5–6 cm. long, 1–3 cm. wide, usually mostly basal, fewer above, pinnately divided, or sometimes only parted; pinnae 5 to 9, ovate, oblique at base, margins crenate; inflorescence terminal, on all stems, tending to give a cymose effect; scorpioid racemes loosening slightly in fruit; flowers nearly sessile; calyx-lobes oblanceolate, 4–6 mm. long, 1 mm. wide, hirsute, glandular, about one-half as long as corolla, scarcely exceeding capsule; corolla campanulate, blue, 7–9 mm. long, and about as broad at top; appendages in corolla triangular, about 1 mm. long and 0.5 mm. broad at top, attached to corolla along hypotenuse, about 0.5 mm. from bottom of corolla, top of appendage denticulate; stamens exserted about 8 mm.; style exserted slightly more than stamens, divided about two-thirds of its length; capsule ovoid, 4–5 mm. long, 3–4 mm. thick, puberulent, slightly glandular, veins showing prominently under lens; seeds somewhat cymbiform, about 4 mm. long, 1–1.5 mm. broad, finely favose but not corrugated, salient ventral ridge quite prominent due to hollowed-out effect on either side, as ventral margins tend to curve inward.

Type locality, Grand Junction, Mesa County, Colorado. Range, southwestern Colorado and perhaps adjacent Utah, from 5000 to 10,000 feet. Specimens representative: COLORADO: Grand Junction, *Eastwood, May 19, 1892* (CA type, C, G, sketch at N), bluffs near Grand Junction, *Stokes, June 15, 1900* (C, N); Lake City, *Pease, July 15, 1878* (N), Rio Mancos, S.W. Colo., *Brandegee in 1875* (G); east of Montrose, *Payson 671* (G); Cimarron, *Baker 71 in part* (N, P, G); Hotchkiss, *Cowen, June 20, 1892* (N).

This plant is most closely related to *P. corrugata*, *P. Bakeri*, and *P. glandulosa*. A collection made by Long in the summer of 1893 (G) illustrates the tendency toward *P. corrugata* in its leaf shape. The seeds of the latter, however, are transversely corrugated on the ventral side, while those of *P. splendens* are not; there is also a tendency for the leaves of *P.*

*corrugata* to be greener, less glutinous and less divided. The relationship of *P. Bakeri* is shown by Brandegee's collection on the Rio Mancos, and by Pease in 1878 in the more stipitate glandular character of their leaves and stems and the slightly more divided leaves. The seeds of *P. Bakeri* are not excavated along sides of the salient ridge as in *P. splendens*. *P. splendens* has been confused with *P. glandulosa* due, principally, to the general misinterpretation of the latter as it differs in habit, type of inflorescence, leaf shape, number and shape of pinnae, size of flower, and seed size.

13. *Phacelia utahensis* n. sp.

A stout erect biennial 4-5 dm. high, herbage viscid-villous with many stipitate glands; leaves narrowly lanceolate, ciliate, lower petioled, upper sessile, margins coarsely dentate, basal cluster thick and matted; inflorescence a crowded thyrus, nearly 3 dm. long; scorpioid racemes dense but soon loose, 2-3 cm. long, usually in pairs; pedicels 1 mm. long; calyx lobes linear or narrow-ob lanceolate, half as long as corolla, only equalling or barely exceeding capsule; corolla blue or violet, rotate-campanulate, 4 mm. long, 4-5 mm. wide; appendages in corolla small, lunate, about 0.5 mm. long, and half as wide, attached less than 0.3 mm. from bottom of corolla; stamens and style exerted 6 or 7 mm.; capsule globose about 3 mm. in diameter; seeds 4, 3 mm. long, foveolate, ventral side excavated on each side of salient ridge, but not corrugated.

Planta erecta, robusta, biennis, 4-5 dm. alta, viscido-villosa, stipitato-glandulosa; foliis anguste lanceolatis, ciliatis, dentatis; infimis petiolatis, superioribus sessilibus; inflorescentia thyrsoides, 2.5-3 dm. longa; racemis scorpioideis, densis, laxis, 2-3 cm. longis, plerumque geminatis; pedicellis 1 mm. longis; lobis calycis linearibus aut angusto-ob lanceolatis, 2-3 mm. longis; corolla probabiliter lavendulacea, rotato-campanulata, 4 mm. longa, 4-5 mm. lata; appendiculis parvis, lunatis, 0.5 mm. longis; staminibus styloque 6-7 mm. exsertis; capsula globosa, circa 3 mm. larga; seminibus 4, 3 mm. longis, foveolatis, facie ventrale excavata at non corrugata, cum porca saliente.

Type from Gunnison, Sanpete Co., Utah, Jones on June 7, 1910 (Pomona College Herb. No. 74223 type).

This plant resembles *P. Palmeri* in habit and general appearance but differs in having a campanulate corolla. It is known only from the type collection.

14. *PHACELIA FORMOSULA* Osterhout, Bull. Torrey Club. 46: 54. 1919.

Erect annual 1.5-2.5 dm. high, rather grayish in aspect, densely hispid or hispidulous, and usually very glandular; stems branching from base or occasionally single, slightly purplish; leaves narrowly ovate or elliptical, 5-7 cm. long, pinnately divided; pinnae 5-10 mm. long, 3-5 mm. wide, entire or den-

tate, the terminal leaflet lobed or pinnatifid, seldom enlarged; inflorescence in rather close panicle on each stem, the entire effect being of a rather rounded cymose type; racemes 2-5 cm. long, moderately compact; pedicel elongating to 1.5 mm. in fruit; sepals lanceolate or slightly oblanceolate, half as long as corolla and slightly exceeding capsule; corolla campanulate, blue or violet, 6 mm. long, 6 mm. wide, lobes entire; appendages broadly lunate, 1 mm. long 0.75 mm. broad, inserted 0.75 mm. from base of corolla; stamens exceeding corolla 2 or 3 mm.; anthers ovoid, 1 mm. long; style exserted 2-3 mm.; seeds oblong, 4 in capsule, 3-4 mm. long, 1 mm. wide, entirely covered with fine pits, ventral surface excavated and divided by salient ridge which is submerged between the incurved edges of the seed.

Type locality, North Park, near Walden, Jackson County, Colo. Range, in Jackson County, Colo. Specimens seen: COLORADO: North Park, near Walden, *Osterhout 5794* type collection (N, P, G), 7286 (P); Walden, North Park, Jackson County, *Keck 889* (P).

15. *PHACELIA GLANDULOSA* Nutt., Journ. Acad. Phila. n. ser. I: 160. 1848.

*Eutoca glandulosa* Hook., Kew Journ. Bot. 3: 293. 1851. *Phacelia deserta* Nelson, Bull. Torrey Club 25: 277. 1898. *P. glandulosa*, subsp. *euglandulosa* var. *deserta* Brand, Das Pflanzenreich IV, 251: 82. 1913.

Erect annual or biennial, 1-3 dm. high, very viscid, glandular, often canescent-pilose; stem stout, usually simple, terete; leaves once pinnately divided 1.5-12 cm. long, 0.5-3 mm. broad, quite leafy at base, lower petiolate, upper with petioles reduced, lanceolate, oblanceolate, or narrowly elliptical; pinnæ 9-21, orbicular, margins entire or crenate; inflorescence terminal, usually in crowded circinate spikes; scorpioid racemes crowded, 1-3 cm. long, lengthening to as much as 5 cm. in fruit; pedicels less than 1 mm. long; calyx-lobes oblanceolate, obtuse, half as long as corolla, scarcely equalling capsule; corolla campanulate, purple, 5-7 mm. long and nearly as broad; appendages in corolla triangular, the altitude of the triangle being nearly as great as the base; stamens exserted 4-5 mm.; style somewhat longer; capsule globose, 3.5 mm. in diameter; seeds 2.5-3 mm. long, 1 mm. wide, favose pitted, ventral surface deeply excavated on each side of salient ridge.

Type locality, about Ham's Fork, Colo. of the West, Lincoln Co., Wyoming. Range, southwestern Wyoming, Montana, Idaho, and northern Utah. Specimens seen: WYOMING: between Opal and Kemmerer, *Payson & Armstrong 3226* (G, R. M., P); Green River, *A. Nelson 3050* (G, N); Georgia Gulch, *Fitch on June 7, 1892* (P); Solon, *Williams in July 1897* (N); Spread Creek, Teton Forest Reserve, *Tweedy 158* (N). MONTANA: Sheridan, *Fitch in June 1895* (P, N). IDAHO: Clayton, Custer Co., *Macbride & Payson 3364* (P, N). UTAH: Henry Mts., Fremont River,

*Cottam 5579* (U); Clear Creek, near Soldier Summit, *Jones 5591* (N); near Glenwood, *Ward 59* (G). The last two cited are atypical.

*P. glandulosa* has been a greatly misinterpreted entity; the name having been applied by Brand and other botanists to material from both sides of the Continental Divide from Wyoming to Mexico including species such as *P. Bakeri*, *P. neomexicana*, *P. denticulata* etc. As interpreted in this paper it is a greatly restricted species characterized by its grayish aspect, round lobes on the pinnae, spicate thyrsus, and usually simple stem and basal cluster of leaves.

16. *PHACELIA SCARIOSA* Brandegee. Proc. Calif. Acad. Sci. 2 ser., 2: 185. 1889.

Annual, 1.5–4 dm. high, erect; stems branching from base, terete or sometimes striate, hispidulous or viscid-pubescent, becoming more glandular toward the top; leaves 3–8 cm. long, petiolate, ovate to elliptical in outline, often pinnately divided or at least deeply cleft or lobed, villous or hirsute; pinnae 3 or 5, oblong, crenate or incised; terminal leaflet usually trilobate and somewhat enlarged; inflorescence irregularly paniculate; racemes loose, often dichotomous; pedicels filiform, 3 cm. long in flower to 10 cm. long in fruit; sepals scarious, villous, fairly glandular, obovate, two-thirds the length of corolla, enlarging and becoming thinner in fruit, 2–4 mm. wide and about 7 mm. long; corolla blue, spreading campanulate, 4 mm. long, 4–5 mm. wide; appendages in corolla narrowly lunate, tapering upward, 1 mm. long, 0.3 mm. wide, attached 0.3 mm. from base of corolla; stamens exserted 1 or 2 mm.; style exserted; seeds 4 in capsule, 3 mm. long, 1.25 mm. wide, slightly cymbiform; dorsal surface favose reticulate; ventral face excavated and longitudinally divided by salient ridge, marked by transverse corrugations.

Type locality, Magdalena Island, Lower California. Range, southern part of Lower California. Specimens seen: LOWER CALIFORNIA: Magdalena Island, *Brandegee on Jan. 12, 1889* (type C, G), *Orcutt 13* (G); Santa Gertrudis, *Purpus 203* and *119* (C, P), Puerto Escondido, *Johnston 4111* (C, G); Agua Verde Bay, *Johnston 3884* (G); Santa Agueda, *Palmer 236* (G); Guaymas, *Palmer 166* (G); San José del Cabo, *Turffer in 1901* (C); 10 miles north of Santa Rosalia, *Reed 6184* (P); San Bartolo, *Jones 24339* (P); La Paz, *Palmer 105* (G), *Jones 24069* (P, G).

17. *PHACELIA PEDICELLATA* Gray, Syn. Fl. II, 1: 160. 1878.

Plant an annual, erect, 1.5–4 dm. high; stems branching from base, or occasionally simple, arising from a rosette of basal leaves, villous, with stipitate glands, and a fine tomentum imbedded in viscid surface below, often striate; leaves suborbicular, ovate or elliptical, usually pinnately cleft or divided 3 or 5 times, viscid-tomentulose, hispid along the veins; pinnae ovate or perhaps

sagittate, incised crenulate or dentate, terminal leaflet enlarged; inflorescence more or less cymose; racemes short, 3–5 dm. long, often dichotomous; pedicels filiform, setose-hispid, 2–5 mm. long; sepals oblanceolate three-fourths as long as corolla, twice as long as capsule, hirsute, becoming scarious in fruit; corolla blue, violet, or white, 5.5 mm. long, 5.5 mm. wide; appendages narrowly lunate or rectangular, if rectangular often also auriculate at base, about 1 mm. long, 0.25 mm. wide, attached 0.5 mm. from base or extending downward to the bottom of corolla; seeds 2.5 mm. wide, 1.25 mm. long, dorsal surface favose-pitted or reticulate; ventral face transversely corrugated, excavated and divided by salient ventral ridge.

Type locality, Lower California. Range, Lower California and adjacent islands, deserts of California and adjacent Nevada and Arizona. Specimens seen: BAJA CALIFORNIA: *Dr. Streets in 1875* type (G); San Luis, *Brandegee on April 27, 1889* (C); western base of Cocupah Mts., on shores of Laguna Magusta, *Epling, Darsie, Stewart, and Robison on Feb. 19, 1933* (P). CALIFORNIA: RIVERSIDE CO., Mecca, *Spencer 2059* (G); Magnesia Springs Canyon, Coachella Valley, *Munz 12012* (P); Shavers Wells, near Mecca, *Munz & Keck 4758* (P). IMPERIAL COUNTY: San Felipe, *Brandegee on Apr. 16, 1895* (C); Fish Mt., *Jaeger on Apr. 10, 1926* (P). SAN DIEGO COUNTY: Palm Creek, near Borego Springs, *Brandegee on Apr. 18, 1895* (C); near Campbells, Vallecito Valley, *Munz & Hitchcock 12089* (P); Palm Canyon, Borego Valley, *Munz 11362* (P). SAN BERNARDINO COUNTY: Old Woman Mts., *Jones on May 13, 1926* (P); Kelso, *Jones on May 2, 1906* (P); Providence Mts., *Brandegee on May 7, 1902* (C); Quail Springs, Little San Bernardino Mts., *Munz 1356* (P). INYO COUNTY: Shepherds Canyon, *Jones on April 30, 1897* (C, P, N); Pleasant Canyon, *Hall & Chandler 6933* (C, P); Funeral Mts., *Coville & Funston 436* (G, N). NEVADA: Rhyolite, Nye Co., *Heller 9628* (G); Amargosa Desert, *Jones on Apr. 17, 1907* (P); Eldorado Canyon at Nelson, Clark Co., *Jones, Apr. 30, 1907* (P). ARIZONA: Yucca, *Jones 20* (G), *Jones on May 15, 1884* (P); Roosevelt Dam, *Eastwood 17400* (G, N); Yucca, *Jones 3938* (G).

Plants from the Death Valley region tend to differ from those farther south by having reddish stems and calyces, narrower and more deeply divided pinnae; but on the whole these differences do not seem consistent enough to merit nomenclatorial recognition.

18. PHACELIA CORRUGATA A. Nelson, Bot. Gaz. 34: 26. 1902.

*P. crenulata* var. *corrugata* (Nelson) Brand, Das Pflanzenreich IV, 251: 79. 1913.

Annual or perhaps a biennial, 1.5–4 dm. high; stem simple or branched from base, erect, somewhat glandular and moderately puberulent; leaves ovate

to narrowly oblong, 1.5–7 cm. long, 1–2.5 cm. wide, from merely repand or sinuate to pinnately lobed, very green, though being somewhat glandular and sparingly hispidulous; inflorescence tending to be cymose; scorpioid racemes 3–5 cm. long in flower, elongating to as much as 15 cm. in fruit; pedicels 1 mm. long, becoming slightly longer in fruit; calyx-lobes 3–4 mm. long, elongating to 5 mm., oblanceolate, sparingly glandular, hispid; corolla deep blue or violet, campanulate, 7–12 mm. long, and about as broad; appendages in corolla broadly lunate, nearly as broad as long; stamens exserted 0.5–0.8 the length of corolla; style equalling stamens; capsule 5 mm. high, ovoid or ellipsoid, about 4 mm. broad, slightly puberulent; seeds 4.5 mm. long, 1.3 mm. wide, finely favose, ventral side excavated on either side of salient ridge, ventral margin and ridge corrugated.

Type locality, Rifle, Garfield Co., Colorado. Range, western Colorado, Utah, and northern Arizona, at 4000–6000 feet. Specimens seen: COLORADO: Rifle, Garfield Co., *Osterhout 2129* type coll. (N); Naturita, western Montrose Co., *Payson & Payson 3861* (G); Paradox, Montrose Co., *Walker 96* (G, N); Palisades, *Crandall 4174* (N); Grand Junction, *Baker 91* (N, P). UTAH: Chepeta Well, *Jones, May 23, 1908* (P); Cisco, *Jones May 2, 1890* (P); Fish Springs, *Jones, June 4, 1891* (P); Green River, *Jones, May 9, 1890* (C, P, N), Detroit, *Jones May 25, 1891* (P); Richfield, Sevier Co., *Jones, June 18, 1889* (P); Price, *Stokes, June 12, 1900* (C, N); Bluff, *Jones May 24, 1919* (P). ARIZONA: near Cameron, *Hanson A230* (N); Clear Creek Canyon, *Ward, May 9, 1901* (N). Western American Plants, *Armstrong 15* (N).

Externally this plant most closely resembles *P. Bakeri* and *P. splendens* however it is easily distinguished from these by seed characters; *P. corrugata* with ventral surface corrugated, and *P. splendens* and *Bakeri* without corrugations. There is a considerable amount of variation in the species, particularly in leaf shape, the more typical form being narrowly oblong and quite green, distribution of leaves being largely basal; this condition varies toward *P. splendens*, and *P. Bakeri* with the leaves ovate, darker, more glandular and distributed throughout the plant.

19. *PHACELIA ORBICULARIS* Rydberg, Bull. Torrey Club 40: 479. 1913.

Erect annual branching from base, 1–2 dm. high, glandular, villous; stem reddish; leaves petiolate, suborbicular, often subcordate at base, margins crenate, 7–15 mm. broad, 8–17 mm. long; inflorescence loosely paniculate, 1 or 2 scorpioid racemes terminating each branch; racemes 1–3 cm. long, loosening in fruit, pedicel less than 1 mm. in fruit; calyx-lobes narrowly elliptical, half as long as corolla, evidently blue or violet, campanulate, 6 mm. long, 4 mm. wide; stamens and style exserted 4–5 mm.; capsule globose, 3 mm. in diameter; seeds 4, 2.5 mm. long, ventral surface excavated on each side of salient ridge and corrugated.



Type locality, Marvine Laccelite, Utah. Specimens seen: UTAH: Marvine Laccelite, *Jones 5663 am* (U. S.) type.

This plant is known only from the type collection, a rather meager specimen. It may or may not be a good species, more material will determine that. It appears to be quite close to *P. corrugata*.

20. *PHACELIA INTERMEDIA* Wooton, Bull. Torrey Club **25**: 457. 1898.

*P. crenulata* Woot. var. *vulgaris* Brand, Das Pflanzenreich IV, **251**: 78. 1913, in part.

An erect annual 1–3 dm. high; stems usually simple, sometimes branching from base, terete or slightly angular, reddish, glandular, hispidulous or finely hirsute; leaves lanceolate or narrowly elliptical, 3–14 cm. long, 0.5–2 cm. broad, crenately lobed, glandularly hispidulous; lobes crenate, terminal lobe not enlarged; inflorescence cymose or paniculate; scorpioid racemes short, about 4 cm. long, loosening in fruit; flowers nearly sessile, pedicels lengthening but slightly in age; sepals lanceolate or narrowly elliptical, half as long as corolla, scarcely exceeding capsule, very glandular and somewhat pubescent; corolla violet, campanulate, 6 mm. long and about as wide, cleft nearly half way; lobes entire; appendages in corolla broadly lunate, transverse portion conspicuous, 0.5 mm. long, 0.5 mm. wide, attached 0.75 mm. from base of corolla; stamens exserted less than 3 mm., style exserted; seeds 4, favose-pitted, 2.5 mm. long, 1.25 mm. wide, slightly cymbiform, ventral face corrugated, excavated and divided by a very prominent salient ridge which often protrudes beyond the ventral outer edges of the seed.

Type locality, Las Cruces, Dona Ana, Co., N.M. Range, western Texas, New Mexico, Arizona and southern Utah from 3500–6000 feet. Specimens seen: NEW MEXICO: mesa west of the Organ Mountains, Dona Ana County, *Wooton on March 10, 1902* (P, C); Mesilla Valley, Dona Ana Co., *Wooton & Standley 3378* (N); Silver City, *Eastwood 8282* (P, G); Bear Mountain, near Silver City, Grant County, *Metcalf 75* (N, P); Berendo Creek, Sierra County, *Metcalf 1567* (N, P, G); Copper Mines, *Wright 1580* (G); Albuquerque, *Jones on April 14, 1884* (N, P). TEXAS: El Paso, *Jones on April 19, 1884* (G, P); El Paso, *Thurber 11 and 146* (N); Sierra Blanca, *Jones 25745* (P). ARIZONA: Fort Verde, *Mearns 260* (N); between Verde & Prescott, *McKelvey 2159* (P); Tanque, Graham County, *Eggleston 19885* (G); Duncan, *Durant in spring of 1920* (P); Stein's, *Jones 18496* (P); Sierra Ancha, *Eastwood 16976* (G); Cedar Glade, *W. W. Jones 16* (G, C). UTAH: Milford, *Jones on June 19, 1880* (P); Marysville, *Jones 5327* (N, P); Frisco, *Jones 2030* (P); St. George, *Jones 5110 af.* (P).

A distinctive plant intermediate between *P. corrugata*, and *P. crenulata*.

**21. *Phacelia texana* n. sp.**

A viscid-villous, glandular biennial 4–5 dm. high; stem stout, erect, terete with many small, simple ascending lateral branches; basal leaves and lower leaves of main stem petiolate, 8–12 cm. long, 2 cm. wide, narrowly lanceolate or oblong, obtuse, margins coarsely sinuate or dentate; other leaves reduced and sessile; inflorescence an expanded spicate thyrsus, 3 dm. long and 2 dm. wide; scorpioid racemes clustered in dense terminal groups on each branch, 2–5 cm. long, in flower; pedicels 1 mm. long or less; calyx-lobes elliptical, one-third as long as corolla, equalling capsule; corolla campanulate, 7–8 mm. long, 6–7 mm. broad, blue or violet; appendages in corolla lunate, upper tip acuminate, attached about 1 mm. above bottom of corolla; stamens and style exerted 4–5 mm.; capsule globose, 2.5 or 3 mm. in diameter; seeds 4, favose-pitted, ventral surface excavated on each side of salient ridge, which is transversely corrugated with alveolate tubercles.

Planta biennis, viscido-villosa, 4–5 dm. alta; caulibus robustis, erectis, teretis, cum ramis lateralibus multibus, parvis, simplicibus, ascendentibus; foliis basalibus et foliis infimis petiolatis, 8–12 cm. longis, 2 cm. latis, anguste lanceolatis aut oblongis, obtusis, sinuatis aut dentatis; foliis superioribus minoribus et sessilibus; inflorescentia spicato-thyrsoidea, 3 dm. longa, 2 dm. lata; racemis scorpioideis densis terminalibusque, constipatis, in anthesi 2–5 cm. longis; pedicellis vix 1 mm. longis; lobis calycis ellipticis, 2–3 mm. longis; corolla campanulata, 7–8 mm. longa, 6–7 mm. lata, violacea aut coerulea; appendiculis lunatis, acuminatis; staminibus styloque 4–5 mm. exsertis; capsula globosa, 2.5–3 mm. longa; seminibus 4, favoso-faveolatis, in porca saliente transverso-corrugatis.

Type from Findlay, Texas. Specimens seen: TEXAS: Findlay, *Jones 285ae on May 5, 1931* (Pomona College Herb. No. 190043 type).

**22. *PHACELIA CRENULATA* Torr., in Wats., Bot. King Exped., 251. 1871.**

Erect annual or biennial 1.5–15 dm. high, glandular pubescent or setose-hispid; stem simple or branching from base; leaves 3–12 cm. long, ovate, oblong or elliptical, basal leaves often conspicuously elongate, pinnately parted or divided or cleft, sometimes only crenate, terminal lobes when present, considerably enlarged; pinnae elliptical, often serrate or dentate; inflorescence cymose or paniculate, scorpioid racemes 2–5 cm. long in flower, lengthening to 8 or 10 cm. in fruit; pedicels to 1 or 2 mm. long; calyx-lobes narrowly elliptical or oblanceolate, 6–8 mm. long; corolla-lobes crenulate; appendages in corolla broadly lunate to rectangular, tapering toward top but usually obtuse; stamens exerted 3.5 or most often 5–6 mm.; style equalling or exceeding stamens; capsule globose, 3–4 mm. in diameter; seeds favose-pitted, 3 mm. long, 1.5 mm. broad, ventral side excavated on either side of salient ridge and marked with prominent transverse corrugations, dorsal side often emarginate with light colored glutinous thickening.

## KEY TO THE VARIETIES OF PHACELIA CRENULATA

1. Plant setose-hispid. Colo. Desert, E. Mohave Desert to S.W. Utah.....22a. var. *ambigua*
1. Plant viscid-glandular.
  2. Inflorescence loosely paniculate. Death Valley.....22b. var. *funerea*
  2. Inflorescence cymose. Mohave Desert northward.....22c. var. *vulgaris*

22a. *PHACELIA CRENULATA* Torr. var. *AMBIGUA* (Jones) Macbride, Cont. Gray Herb. 49: 25. 1917.

*P. ambigua* Jones, Cont. Western Bot. 12: 52. 1908. *P. crenulata* Torr. var. *vulgaris* Brand, Pflanzenreich, IV, 251: 78. 1913, in part.

Erect annual 1.5–4 dm high; stems erect, usually branching freely from the base, terete or occasionally angled, heavily coated with long, white stiff hairs which are often glandular; leaves pinnately divided or deeply cleft, sometimes only dentate or sinuate, ovate, elliptical, oblanceolate or lanceolate in outline, setose hispid, glandular; pinnae 5–11, terminal lobes often enlarged and trilobate; margins of pinnae may be cleft or irregularly dentate or merely crenate or sinuate; inflorescence variable, from 3–8 or 9 racemes in a cluster, usually cymose; scorpioid racemes loosening in fruit and lengthening to 6 or 7 cm.; flowers sessile; pedicel elongating to 1 or 2 mm. in fruit; sepals narrowly ovate or oblanceolate, densely hispid, especially on veins and edges, half as long as corolla, slightly exceeding capsule; corolla blue or violet, spreading-campanulate, 6–7 mm. long, 5 mm. wide, lobes crenulate to nearly entire; corolla appendages rectangular, 1.5 mm. long, 0.5 mm. wide, attached 0.75 mm. from base of corolla; stamens mostly exserted about 5 mm., sometimes three exserted and two just equalling corolla; style equalling or barely exceeding stamens.

Type locality, Needles, Calif. Range, Colorado Desert and northward along the Colorado River. Specimens seen: BAJA CALIFORNIA: Los Angeles Bay, Gulf of California, *Palmer 592* (G). CALIFORNIA: SAN DIEGO COUNTY: Borrego Springs, *Brandegee, April 17, 1895* (C); San Felipe Creek, *Eastwood 2722* (N). IMPERIAL COUNTY: Mesquite, *Parish 760* (G); Signal Mountain, *Brandegee Mar. 30, 1901* (C). RIVERSIDE COUNTY: Palm Springs, *Eastwood 3040* (G); Mecca, *Spencer 1581* (P, G); Dos Palmas Spring, *Munz 9958* (C, P). SAN BERNARDINO COUNTY: The Needles, *Jones 3822* type coll. (P, C, N); Barnwell, *Brandegee, May 1911* (C). NEVADA: Good Springs, *Jones April 30, 1905* (P); Vegas Wash, *Tidestrom 8983* (N). UTAH: "Southern Utah," *LeRoy 332* (N); St. George, *Parry 180* (N, G). ARIZONA: Tucson, *Toumey April 3, 1892* (C, N); Beavertdam, *Jones 5018* (C, N, P); Grand Canyon, *Gray in 1885* (G); Picacho Peak, Pinal County, *Gillespie 8896* (N); Salt River Mountains, Maricopa County, *Gillespie 8844* (G, N).

This variety, common in the California Desert and eastward, intergrades with *P. crenulata* var. *vulgaris* in the northern part of its range.

22b. *PHACELIA CRENULATA* Torr. var. *FUNEREA* J. Voss ex Munz, Man. So. Calif. Bot., 409, 600. 1935.

Annual or biennial 2–15 dm. high, extremely glandular and glandular puberulent; stem simple, occasionally branching from base, usually deep red to nearly purple in color; leaves 3–12 cm. long, ovate, oblong, or elliptical, crenate or often pinnately divided, when divided, terminal lobes enlarged with margins somewhat irregularly dentate or crenate; inflorescence paniculate; scorpioid recemes 2–5 cm. long, lengthening considerably in fruit; pedicels 1 mm. long; calyx-lobes elliptical or oblanceolate, reddish or purple tinged, particularly on midribs, 3 mm. long; corolla blue or pale purple, or occasionally a deep violet, rotate-campanulate, 6–7 mm. long and about as broad, lobes crenulate; appendages in corolla broadly lunate; stamens exerted 3.5–6 mm.; style as long as or longer than stamens; capsule globose, 3–4 mm. in diameter; seeds favose pitted, ventral surface corrugated, salient ridge prominent, dorsal side often emarginate.

Type locality, Black Canyon, White Mts., Calif. at 5700 ft. alt. Range, region of Death Valley, California and Nevada. Specimens seen: CALIFORNIA: MONO COUNTY: Black Canyon, White Mts., *Duran* 561, type collection (C, R.S.A., P, N); INYO COUNTY: 2 mi. west of Darwin, *Munz* 12483 (P); Darwin, *Jones*, Apr. 28, 1897 (N); summit of Mt. Baldy, above Wildrose Canyon, *Hoffmann* 458 (P); Westgard Pass, *Ferris & Bacigalupi* 8062 (C, P). NEVADA: ESMERALDA COUNTY: Cold Mt., *Purpus* 5976 (C); summit of Gold Mt., *Keck* 576 (P); LINCOLN COUNTY: Calientes, *Jones*, Apr. 29, 1904 (P). SOUTHERN UTAH or NORTHERN ARIZONA: *Palmer* 332 (G).

22c. *PHACELIA CRENULATA* Torr. var. *VULGARIS* Brand, Das Pflanzenreich IV, 251: 78. 1913.

Plant 1.5–5 dm. high, usually branching from base, moderately glandular and glandular pubescent; stem green or yellowish; inflorescence cymose.

Type locality, Trinity Mts., Nevada. Range, Mohave Desert region. Specimens seen: CALIFORNIA: INYO COUNTY: Funeral Mts., Death Valley, *Jones* Apr. 9, 1907 (P); Emigrant Pass, *Hitchcock* 12, 324 (P); Furnace Creek, Ryan, *Munz & Hitchcock* 11025 (P); Panamint Canyon, *Jones* May 3, 1897 (P); Inyo, *Rixford* in 1890 (C). SAN BERNARDINO COUNTY: Box "S" Ranch, Mohave Desert, *Munz & Hitchcock* 12770 (P); 10 mi. S.W. Garlic Springs, *Munz & Keck* 7885 (P); Barstow, *Munz*, 2577 (P); 5 mi. N. of Barstow, *Johnston* 6523 (P); Daggett, *Brandege* in May 1913 (C). NEVADA: CHURCHILL COUNTY: Trinity Mts., *Watson* 873, in May 1868 type collection (G, N); WASHOE COUNTY: *Lemmon* 825 (G); Pyramid Lake, *Lemmon* May 1879 (G), June 1879 (N);

Pyramid Lake, *Kennedy 1039* (C, P); MINERAL COUNTY: Base of Mt. Grant, *Heller 10900* (G, C, N); NYE COUNTY: Tonopah, *Shockley 11* (C); *153* (P); LINCOLN COUNTY: Good Springs, *Jones May 1, 1905* (P); Kernan, Meadow Valley Wash, *Goodding 658* (G, N); CLARK COUNTY: *Goodding 2195* (G); ESMERALDA COUNTY: Palmetto Range, *Purpus 5859* (C, N, P). UTAH: St. George, *Cottam 5656* (U); Marysville, *Jones 5327* (C); Frisco, *Jones 2030* (P); Geaver Valley, *Palmer 332* (N).

23. *PHACELIA MINUTIFLORA* Voss ex Munz, Man. So. Calif. Bot., 409, 600. 1935.

Erect annual 1.5–3 dm. high, branching freely from base, or occasionally branching at base, rather heavily glandular, sometimes viscid toward the base, the gray puberulence intermixed with longer stiffer hairs and somewhat darkened by the many stipitate glands; stems yellow, green or purple; leaves ovate or oblong, commonly 5-pinnate, 1–6 cm. long, 1–3 cm. broad, 3 terminal pinnae each about twice as large as others; inflorescence rather cymose; scorpioid racemes in numerous terminal clusters of 2 or 3, with a tendency toward dichotomy; pedicels less than 1 mm.; calyx-lobes 3–4 mm. long, lanceolate, ciliate, hirsute, moderately glandular; corolla campanulate, purple, 3–4 mm. long, 3–4 mm. wide, appendages in corolla lunate, 0.75 mm. long, 0.25 mm. wide, attached 0.5 mm. from bottom of corolla; stamens and bifurcate style exerted 1.5 mm.; capsule globose, 3.25 mm. in diameter; seeds 4, 3 mm. long, 1.5 mm. wide, faveolate, ventral surface excavated on either side of salient transversely corrugated ridge.

Type locality, 2 miles north of Cargo Muchacho Mountains eastern Imperial County, Calif. Specimens seen: CALIFORNIA: IMPERIAL COUNTY: 2 mi. north of Cargo Muchacho Mts., *Munz & Hitchcock 12141*, type (P); Signal Mountain, *Abrams 3190* (G, P); Colorado Desert, *Brandegge in April 1905* (C); SAN DIEGO COUNTY: San Felipe Creek, Colorado Desert, *Eastwood 2722* (G); SAN BERNARDINO COUNTY: north end of Whipple Mountains, *Munz & Harwood 4553* (P). ARIZONA: Wickenburg, *Palmer 626* (N, G).

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# The origin and development of the foliage leaves and stipules of *Morus alba*<sup>1</sup>

G. L. CROSS

(WITH SIXTEEN FIGURES)

In a recent paper the writer (Cross, 1936) has described the origin and developmental behavior of the bud scales of *Morus alba* L. The present paper contains a description of comparable phenomena in the growth of the foliage leaves and stipules, with suggestions concerning the morphological interpretation of these structures in the genus.

The classic interpretation of bud scales, i.e. that they represent metamorphosed foliage leaves, has been challenged by Foster (1928, 1935a, 1935b), who, in a series of papers, has established beyond doubt that the problem is worthy of further investigation. He points out in particular the dearth of information concerning the early developmental stages and histogenesis of bud scales, and he has provided the only detailed comparative account of foliage leaf and bud scale histogenesis.

The generally accepted interpretation of stipules is that they are lateral divergences of the base of the foliage leaf. In a recent paper Ponzo (1934) has presented evidence in favor of the theory of an independent phylogenetic origin of foliage leaves and stipules. As far as the present writer has been able to discover, there is no paper dealing with the histogenesis of stipules to be found in the literature. While ontogeny as a criterion of phylogenetic relationship should certainly be used with caution, it does have its place as a source of evidence, and it is extremely doubtful if foliar structures can be given a satisfactory phylogenetic interpretation in the absence of knowledge concerning their ontogeny.

For the reader's convenience, a brief summary of the origin and development of the bud scale will be given. The growing point of *Morus alba* L. consists of a two-layered tunica and a central corpus. The outer tunica layer is called T-1, the inner T-2. The bud scale is initiated by periclinal divisions in T-2 and outer corpus. Most of the scale is derived from the tunica, however, for the corpus contributes only slightly to the basal portion. The bud scale grows in length through the activity of apical and subapical rows of initials. Growth in width is accomplished by the division of marginal and submarginal rows of initials which converge upward to the apical and subapical rows. This mode of growth is strikingly suggestive of that found commonly in leptosporangiate ferns. Procambial tissue dif-

<sup>1</sup> Contribution from the Botanical Laboratory of the University of Oklahoma, n. s. 41.

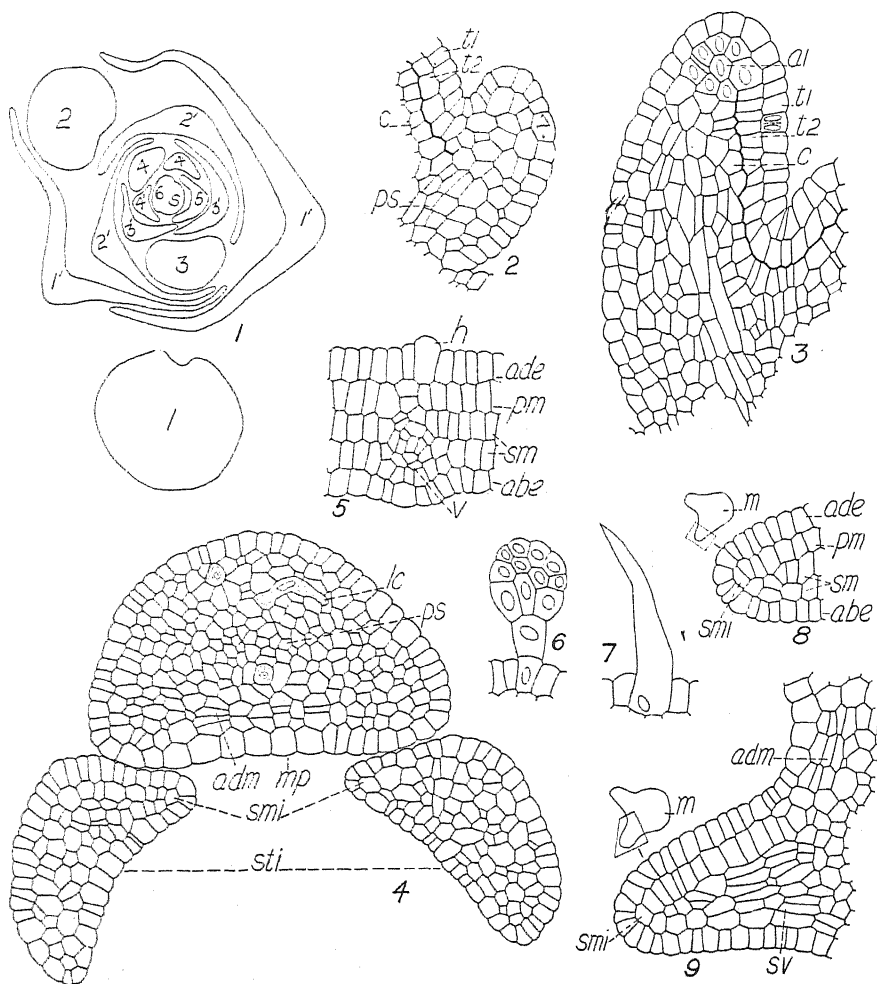


Fig. 1. Transverse section through stem tip, petioles and stipules of *Morus alba* L. Note the slightly asymmetrical, alternate phyllotaxy; 1, petiole; 1', stipules associated with petiole 1; 2, 2' same as 1, 1', etc.; 5, leaf base below point of divergence of stipules and midrib; 6, very young foliage leaf primordium before divergence of stipules from midrib; s, stem tip.  $\times 30$ .

Fig. 2. Longitudinal section through portion of growing point and foliage leaf primordium ( $85\mu$  high, measuring from juncture of abaxial surface and stem); t1, outer tunica; t2, inner tunica; c, corpus; ps, procambial tissue that will become the median leaf trace.  $\times 325$ .

Fig. 3. Longitudinal section through portion of growing point and older foliage leaf primordium ( $170\mu$  high); ai, apical initials; t1, derivatives of outer tunica; t2, derivatives of inner tunica; c, corpus.  $\times 325$ .

Fig. 4. Transverse section through young midrib ( $140\mu$  high) and stipular pri-

ferentiates very late, when the scale is 800–900 $\mu$  high. Stiff, appressed dorsal hairs of but one type were found. Latex canals were not found in scales of any size or age.

#### THE INITIATION AND DEVELOPMENT OF THE FOLIAGE LEAF

General aspects of the development of foliage leaves have been extensively investigated. In 1853 Trécul reported that the sheath appears first, then the blade, and finally the petiole. Eichler (1861) distinguished a very early "Primordialblatt" which segments into a leaf base and upper leaf. He reported that the leaf base may form stipular appendages and that the sheath, when present, arises secondarily from the leaf base by intercalary growth. The upper leaf produces the petiole and lamina. The petiole originates from a zone of meristematic tissue between the lamina and base, in many instances after the lamina has undergone extensive development. In no case, according to Eichler, does petiole development precede laminar differentiation. This order of development has been confirmed by numerous investigators. Foster (1935a) Noack (1922) and Avery (1933) have provided recent information concerning the histogenesis of foliage leaves.

*The primordium.* The primordium of a foliage leaf of *Morus alba* appears as a hemi-elliptical mass of cells at the side of the stem tip, and it closely resembles a bud scale primordium of comparable age. A comparison of the young leaf in figure 2 with a bud scale (Cross 1936, figs. 4, 5) will emphasize the similarities of the two organs in longitudinal view. For the reader's convenience heavy lines delimiting the tunica and corpus have been drawn. Both primordia are initiated by periclinal divisions in T-2 and in the outer corpus. The primordium of a foliage leaf may, however,

mordium (70 $\mu$  high); *mp*, midrib primordium; *sti*, stipular primordia; *lc*, latex canal; *ps*, procambial strand; *adm*, adaxial meristem; *smi*, submarginal initials.  $\times 325$ .

Fig. 5. Transverse section of portion of blade of young leaf (about 20 mm. wide); *ade*, adaxial epidermis; *h*, hair; *pm*, palisade meristem; *sm*, spongy meristem; *abe*, abaxial epidermis; *v*, veinlet.  $\times 325$ .

Fig. 6. Clavate epidermal hair of type found on both surfaces of foliage leaf.  $\times 325$ .

Fig. 7. Unicellular hair of type found on both surfaces of foliage leaf, both surfaces of stipule, and abaxial surface of bud scale.  $\times 325$ .

Fig. 8. Transverse section through margin of lamina of young foliage leaf (500 $\mu$  high), about 250 $\mu$  above base; *m*, midrib; *ade*, adaxial epidermis; *pm*, palisade meristem; *sm*, spongy meristem; *abe*, abaxial epidermis; *smi*, submarginal initial.  $\times 325$ .

Fig. 9. Transverse section through margin of lamina of young foliage leaf (500 $\mu$  high) about 120 $\mu$  above base; *m*, midrib; *smi*, submarginal initial; *adm*, adaxial meristem; *sv*, origin of secondary vein. (The stipules associated with this leaf were about 275 $\mu$  high.)  $\times 325$ .



be distinguished from that of a bud scale by a study of the adjacent corpus. If the primordium is to develop into a foliage leaf, a procambial strand which will develop into the median leaf trace of the trilacunar node will be found in the corpus before the primordium has attained a length of  $75\mu$  (fig. 2). In contrast, the procambial tissue of a bud scale does not appear until the organ has grown to a height of several hundred microns.

Further growth of the foliage leaf primordium differs markedly in several respects from that of the bud scale. The bud scales increase in length through the activity of apical and subapical rows of initials (each cell with two cutting faces) which have been derived from T-1 and T-2 respectively. The corpus does not contribute to the tissues of the scale, except perhaps very slightly to the extreme basal portion. The foliage leaf primordium shows no indication of the formation of apical or subapical initials with two cutting faces, but increases in length through the activity of a subapical group of irregularly shaped cells (fig. 3), supplemented by cell divisions throughout the organ. The young epidermis adjusts itself to increase in length by anticlinal division and surface growth. In contrast to the bud scale, the foliage leaf receives a distinct contribution of tissue from the corpus (fig. 3). Figure 3 shows the continuity of T-1, T-2 and the first layer of the corpus, with their derivatives in the lower adaxial region of the primordium. It is obvious from this illustration that the corpus is definitely involved in the origin of the foliage leaf, although a line delimiting the tunica and corpus cannot always be drawn at the tip or along the abaxial surface. This situation parallels that of the foliage leaf of *Carya Buckleyi* var. *arkansana*, as described by Foster (1935a).

The foliage leaf primordium broadens until from one-third to one-half of the circumference of the stem tip is involved. Marginal growth is at all times quite unlike that exhibited by the bud scale primordia. Marginal and submarginal initials with two cutting faces are never formed, but growth in width, like growth in length, occurs through the activity of irregularly dividing cells at the edges and throughout the young leaf.

*The blade and petiole.* Growth in length of the foliage leaf primordium occurs uniformly until a height of about  $70\mu$  is attained. Then a suppression of growth occurs at two points on the terminal ridge, one on each side of the apex. The two points of suppressed growth separate three persistent meristematic areas, one median and two lateral. These grow rapidly and a central, dominant conical structure flanked by two lateral papillae is produced (fig. 4). The central conical structure is the primordium of the midrib of the foliage leaf and from it will develop the leaf blade and petiole. The lateral papillae are the primordia of the stipules. The basal portion of the primordium upon which these three structures are borne could be in-

terpreted as the leaf base. The behavior is similar to that of *Tilia grandiflora* (Mikosch, 1876) and is probably characteristic of plants which produce free lateral stipules.

The primordium of the midrib enlarges by general cell divisions until it becomes somewhat triangular in transections, with a flat adaxial surface and convex abaxial surface (fig. 4). Detailed studies of the histogenesis of the midrib were not made, though careful observations of a number of sections indicate that the phenomena associated with the growth and differentiation of the midrib and petiole of *Morus* agree closely in their grosser aspects with Foster's description of the leaf of *Carya*. A procambial arc appears in the petiolar midrib region. Early in the ontogeny of this region there is developed an adaxial meristem (fig. 4), which, although it does not produce a conspicuous bulge on the ventral surface of the primordium as figured by Foster (1935a) for *Carya*, contributes materially to radial increase in thickness of the primordium. The adaxial meristem persists until the laminar portions of the foliage leaf are in an advanced stage of development (fig. 9). Some of its derivatives become procambial tissue which close the procambial arc in the lower midrib and petiole.<sup>2</sup> It is worthy of note that latex tubes begin to form in the midrib at a very early stage (fig. 4). This seems significant, because although latex tubes occur abundantly in the foliage leaf and stem, they were never found in bud scales or stipules.

When the midrib primordium has attained a height of approximately  $200\mu$  the lamina meristem appears as two ridges on its adaxial margins. Ventral, marginal growth of the midrib primordium is accelerated slightly above the juncture of the primordium with the leaf base, and the halves of the lamina (which probably arise from T-2) diverge from each adaxial margin of the midrib as a ridge of tissue five layers of cells thick (fig. 8). The two ridges are initiated near the basal portion of the midrib, but they soon develop acropetally until all of the midrib except the extreme basal portion is involved. The basal portion of the midrib primordium, where the lamina meristem does not develop, has a constricted appearance. By intercalary growth it finally forms the petiole.

The marginal growth of the lamina of the foliage leaf is entirely different from that exhibited by the bud scale. Lateral growth of the bud scale is due to the activity of a row of wedge-shaped initials on each margin, supplemented by the divisions of similarly constructed submarginal rows of initials (Cross, 1936). Lateral growth of the foliage leaf blade can be best understood by reference to figures 8 and 9. The epidermis of the ventral

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and dorsal surfaces is continuous over the edge of the lamina; and all cells are meristematic. No distinction based upon mitotic activity was noted between the cells of margin and those of the dorsal or ventral surface; therefore it has not been possible to distinguish marginal initials. This is somewhat in contrast to the situation described by Foster (1935a) for the foliage leaf of *Carya*. Immediately within the epidermis in figures 8 and 9 may be seen a wedge-shaped submarginal initial which is a member of a submarginal row of similarly constructed initials. From the submarginal initial two rows of cells diverge and form the subepidermal layers of the abaxial and adaxial surfaces. This type of submarginal growth is characteristic of bud scales and stipules in their younger stages. It persists in the foliage leaf until the margins mature. Further study of figures 8 and 9 reveals that the abaxial subepidermal layer splits periclinally, two or three cells removed from the submarginal initial, thus forming the median layer and abaxial subepidermal layer of the five-layered blade. From these figures and from the study of many other leaf margins it would seem that marginal growth, with the exception of increments to the epidermis, occurs through the activity of a submarginal row of wedge-shaped initials which cut off segments alternately to the abaxial and adaxial surfaces of the leaf, and that the middle layer of the leaf arises from a periclinal splitting of the abaxial segments. This mode of marginal growth is unlike, in most respects, that of the bud scale. It is similar to the situation obtaining in *Carya* (Foster, 1935a), but differs from the types described for *Pelargonium* (Noack, 1922) and *Nicotiana* (Avery, 1933). As mentioned by Foster (1935a, footnote 11, p. 122) there is a "need for further comparative investigations" of the marginal growth of foliage leaves.

Marginal growth of the leaf persists until shortly after the buds have expanded. Before the leaves have unfolded, however, the tip of the leaf begins to mature, and from this point maturation proceeds basipetally along each margin of the leaf. The apex and margins of a leaf 20 mm. in width are completely non-meristematic, with highly vacuolated cells. These observations are in accordance with Avery's (1933) report for *Nicotiana*. The adaxial epidermal layer of the midrib begins maturation very early, before the origin of the lamina (fig. 4), but the abaxial epidermal layer retains its meristematic character at least until the leaf is half grown. This behavior of the epidermis was reported for *Carya* (Foster, 1935a) and is probably widespread in the leaves of angiosperms. The mesophyll of a leaf 20 mm. in width is still actively meristematic and no trace of differentiation or maturation is detectable (fig. 5).

The secondary veins arise in the blade almost immediately after the

marginal meristem has become well organized and the five-layered nature of the young blade can be distinguished (fig. 9). The procambial tissue of the secondary veins arises through extensive periclinal divisions in the middle, and the abaxial subepidermal layers of the blade. Such periclinal divisions approach within four or five cells of the margin. Except for the secondary veins and veinlets, the blade remains five layers of cells thick until maturity, a situation previously described and figured by Smith (1934) for *Morus alba*.

The vernation is variable. Usually the blade develops with the adaxial surfaces of its halves opposing each other, though occasionally the halves grow more laterally and a leaf with a flat or only slightly concave adaxial surface is produced.

Shortly after the lateral wings of the young blade are differentiated, growth may be suppressed at one or more points along either margin. These points of growth suppression result in the production of the lobes which occur sporadically in the leaves of the white mulberry. The growth suppression may be partial or complete and the notch is correspondingly shallow or deep. The position of all notches is determined at a very early stage in the ontogeny of the leaf, almost immediately succeeding the differentiation of the lamina.

Veinlets are differentiated as the lamina continues to grow. These appear in the laminar regions between the secondary veins where the tissue is five layers of cells thick. The outer two of the five layers become the adaxial and abaxial portions of the epidermis. The intervening three layers produce the mesophyll and veinlets. The adaxial subepidermal layer produces the palisade tissue, while the median and abaxial subepidermal ones differentiate into spongy mesophyll. The differentiation of the mesophyll occurs very late in the ontogeny of the leaf, the palisade and spongy portions remaining meristematic until after bud expansion. The late differentiation and maturation of the tissues of the leaf exclusive of the veins is in direct contrast to the early differentiation and maturation of comparable tissues in the bud scale (Cross, 1936). It will be shown later that it also contrasts with the early maturation of the tissues of the stipules.

An interesting feature of the foliage leaf of *Morus* is the type and distribution of its epidermal hairs. Two types are found: unicellular, stiff, appressed hairs, of the type found on bud scales (fig. 7); and multicellular, glandular, clavate ones (fig. 6). Both types are found on either surface of the foliage leaf, although more abundantly on the abaxial surface. Hairs of but one type were found on the bud scale, and only on the abaxial surface.

## THE DEVELOPMENT OF STIPULES

Stipules have provided a source of botanical speculation and research since the time of Grew. They have been variously interpreted as products of the leaf base, as independent organs, as the lateral leaflets of a tri-compound leaf, as the lowest lobes of a lobed leaf, and as the lowest teeth of a serrate leaf. Agardh (1849), and later Clos (1879) concluded that stipules are not a part or outgrowth of the leaf with which they are associated, but that they are independent organs homologous with the adjacent leaf. This interesting conception of stipules has not received general support from botanists. Ontogenetic studies of the leaf by Trécul (1853) revealed that stipules arise from the base of the foliage leaf primordium; and Colomb (1887) reported that the vascular strands which supply the stipules are always branches from one or more of the lateral leaf traces. Such researches suggest that stipules are to be regarded as products of the leaf base.

Among the earliest generalizations concerning stipules is that of Eichler (1861) who states: "Die Entstehung der Stipulä aus dem Blattgrund ist das wesentlichste Moment zu ihrer Charakterisierung. Sie sind diesem zufolge stets als wirkliche Teile des Blattes, an dessen Grund sie stehen, zu betrachten und nicht als besonders den Blättern koordinierte Gebilde." Mikosch in 1876 described the origin of the stipules of *Tilia grandiflora* but his studies were made in connection with an attempt to determine the foliar nature of the bud scales in that species, and a detailed statement concerning the ontogeny of the stipules was not made. His report states that the foliar primordium of *Tilia* segments very early into lateral stipules, and a median portion which will become the petiole and blade; and he concluded from this that the stipules are to be regarded as lateral outgrowths from the leaf base. The bud scale consists of the two stipules "fused" with the leaf, according to his account.

It is interesting to note that this interpretation of the bud scale of *Tilia* is in agreement with Henry's (1846) earlier interpretation of the bud scales of *Morus scabra*; although Henry implies that the leaf is perhaps not involved in the fusion, and that the bud scales may consist of two fused stipules. In the latter case the development of the leaf would necessarily be suppressed.

Sinnott and Bailey (1914) have provided one of the more recent papers on stipules. Their work is based upon extensive studies of nodal anatomy, however, and the ontogeny of the foliar organs is not considered. They find that families of plants that possess unilacunar nodes usually lack stipules. Families possessing trilacunar nodes usually show two stipules asso-

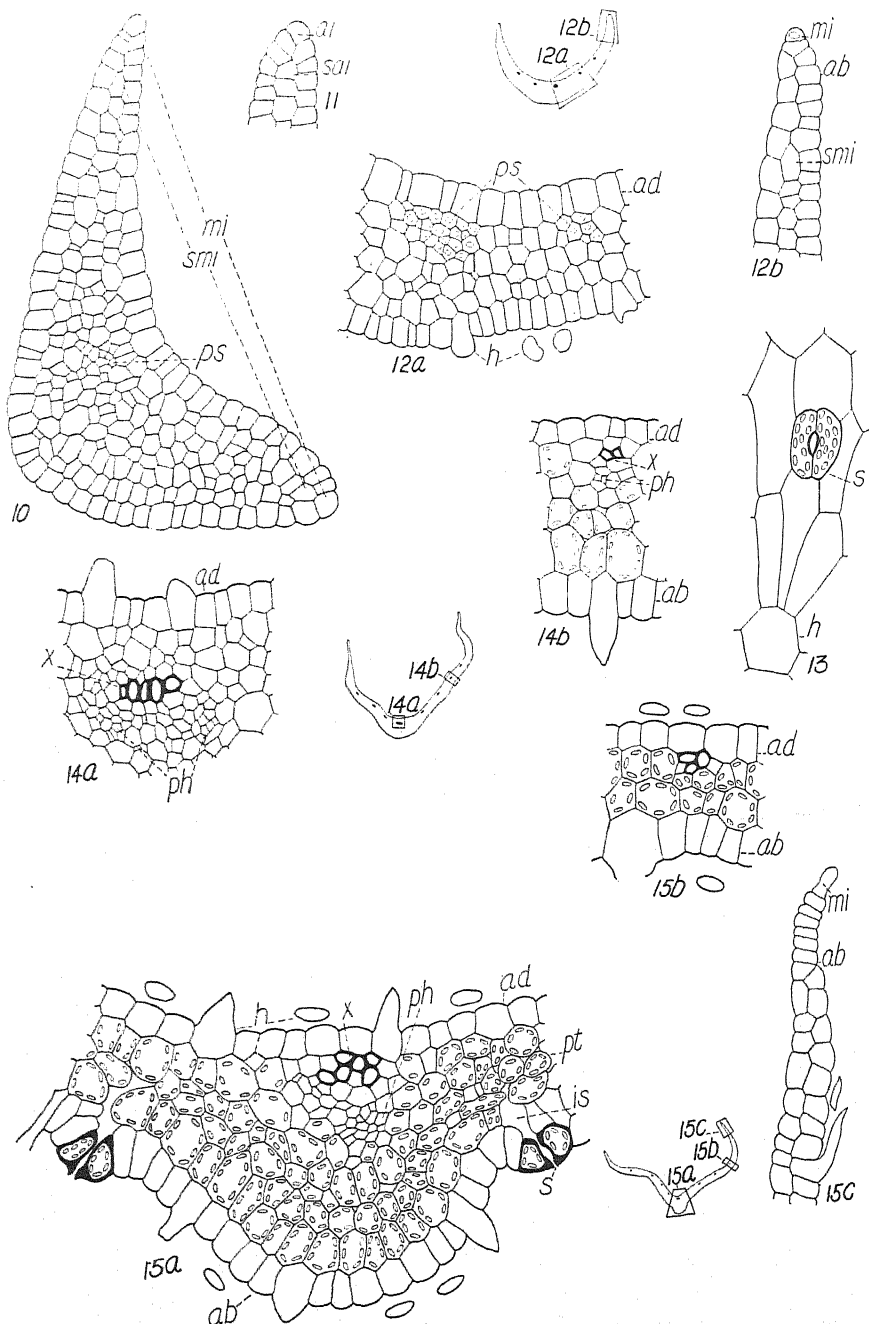
ciated with each leaf, and families with multilacunar nodes usually possess sheathing leaf bases. They regard the trilacunar node as being the most primitive, and suggest that the presence of the lateral leaf traces of the trilacunar type may stimulate the formation of stipules. Concerning the foliar nature of the stipule, they mention that forms possessing these organs practically always have serrate or toothed leaves and that forms with entire leaves usually lack stipules regardless of their nodal anatomy. From this they infer that stipules may be regarded as the two earliest leaf-teeth, the position of which may have been determined by the position of the two lateral leaf traces, rather than by the vascular bundles of the lamina.

In summarizing their work, Sinnott and Bailey say that anatomical facts "favor the contention that stipules are integral portions of the base of the leaf, a view which is well expressed by Eichler when he says that stipules arise without exception as a product of the leaf-base of the primordial leaf. Anatomical facts are also in agreement with the theory frequently put forward that stipules, the sheathing leaf-bases, the ochrea, the stipular appendages of the lower monocotyledons and the tendrils and ligules of the higher ones are morphologically identical, for the character and position of these various structures is to a large extent dependent on the type of nodal topography."

The interpretation of Eichler (1861), supported by Sinnott and Bailey (1914), is now prevailingly accepted by botanists. With the exception of Ponzo (1934) most modern workers apparently regard stipules as divergences from the base of the foliage leaf. Detailed summaries of the literature pertaining to stipules have been provided by Domin (1911a), Glück (1919) and Schrödinger (1919).

It seems unfortunate that so little attention should have been given to comparative histogenetic studies of the various foliar organs. Apparently no complete account of the stipular histogenesis of any species has appeared. The present writer has been able to find only two references to the mode of early growth of stipules. Noack (1922), in connection with his description of the early histogenesis of the foliage leaf of *Pelargonium*, makes the following brief comment: "Schliesslich sei noch erwähnt, das auch die Nebenblätter, die im erwachsenen Zustand vier Mesophyllschichten besitzen, genau den gleichen Wachstumsmodus auf dem Querschnitt der Anlage zeigen. Auch ihre Fläche vergrössert sich durch typisches Randwachstum der subepidermalen Zellen." From this one would expect to find that the stipules and foliage leaves of *Pelargonium* exhibit similar features of growth and development, at least in their earlier stages. Schüepp (1931) in his report on *Lathyrus* briefly states: "Die charakteristische Umrissform





Figs. 10-15c (See opposite page for explanation.)

des pfeilförmigen Nebenblattes würde abgeleitet aus den Gegensätzen im Wachstum von Blattspitze und Blattbasis. Die Blattspitze zeigte ein starkes Vorwiegen des Längenwachstums gegenüber dem Breitenwachstum und ginge als 'Vorläuferspitze' (Goebel) frühzeitig in den Dauerzustand über. In der Blattbasis überwiegte das Längenwachstum nur wenig gegenüber dem Breitenwachstum; dagegen dauerte hier das Wachstum lange Zeit fort und bildete den Hauptteil der Blattfläche."

The stipule initials of *Morus alba* undergo a decidedly different ontogenetic development from that of the foliage leaf, but they exhibit certain features of development which are strikingly suggestive of bud scale histogenesis. The stipular primordia diverge laterally from the leaf base when the latter is about  $70\mu$  high. Immediately preceding their divergence, only one procambial strand (the midrib of the foliage leaf) is to be found in the leaf base. Shortly after the stipular primordia become distinct, a procambial strand differentiates in the leaf base a few microns below each stipule. These strands, when traced downward, are found to enter the procambial ring of the stem on opposite sides, i.e., 180 degrees apart. They constitute the lateral leaf traces of the trilacunar node. The fact that the lateral leaf traces differentiate subsequent to the formation of the stipular primordia would seem to make less tenable the suggestion of Sinnott and Bailey (1914) that lateral traces of the trilacunar node influence the production of stipules.

The young stipules grow rapidly in length and width and at an early stage become longer than the foliage leaf. Their histogenetic development is entirely unlike that of the foliage leaf, but is strikingly similar to the type described for the bud scale (Cross, 1936). Figure 4 shows a transection of

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Fig. 10. Transverse section through a young stipule ( $275\mu$  high) about  $24\mu$  from the base; *mi*, marginal initials; *smi*, submarginal initials; *ps*, procambial strand.  $\times 325$ .

Fig. 11. Longitudinal section through a young stipule ( $275\mu$  high); *ai*, apical initial; *sai*, subapical initial.  $\times 325$ .

Figs. 12a-12b. Portions of a transverse section about  $192\mu$  above the base of a stipule (about  $800\mu$  high); *ps*, procambial strand; *h*, hair; *ad*, adaxial epidermis; *mi*, marginal initial; *smi*, submarginal initial; *ab*, abaxial surface.  $\times 325$ .

Fig. 13. Surface view of the epidermis of a mature stipule; *s*, stoma with guard cells; *h*, base of hair.  $\times 325$ .

Figs. 14a-14b. Portions of a transverse section about  $500\mu$  above the base of a stipule (about 3 mm. high); *ad*, adaxial epidermis; *x*, protoxylem element; *ph*, phloem; *ab*, abaxial epidermis.  $\times 325$ .

Figs. 15a-15c. Portions of a transverse section about  $1000\mu$  above the base of a stipule (about 3 mm. high); *ad*, adaxial surface; *ab*, abaxial surface; *h*, hair; *x*, xylem; *ph*, phloem; *pt*, photosynthetic tissue; *is*, intercellular space; *s*, stoma with guard cells; *mi*, marginal initial, extending to form a hair.  $\times 325$ .

a pair of young stipular primordia shortly after they have diverged from the leaf base. The edges of the primordia show definite indication of activity. Although marginal initials have not been organized, submarginal initials of the type described for bud scales (Cross, 1936) are recognizable. Provascular tissue and latex canals, although conspicuous in the primordium of the foliage leaf, are lacking in the stipular primordia.

The mode of marginal growth may be better understood from a study of figure 10. Here marginal initials are conspicuous on either edge of the stipule, although they appear to have been functioning for a greater length of time on the margin distal to the foliage leaf. Each marginal initial represented in figure 10 is a member of a row of initials which diverge from a similarly constructed row of apical initials (fig. 11). The initials are wedge-shaped and cut off segments alternately to the adaxial and abaxial surfaces of the stipule.

Submarginal initials are likewise well organized in figure 10. Studies of serial sections show that these cells are members of submarginal rows which diverge from a subapical row (fig. 11) at the apex of the stipule. The function of the submarginal and subapical initials in the growth of the stipule may be seen by reference to figures 12a and 12b, where, by transverse divisions, these cells have given rise to a plate-like core of tissue enclosed by the young epidermis. Exactly the same mode of apical and marginal growth has been described for the bud scales of *Morus* (Cross, 1936). Although the margin of the stipule distal to the foliage leaf grows more rapidly at first (fig. 10), the proximal margin soon develops rapidly enough so that a symmetrical organ is produced. The proximal edges of each member of the pair of young stipules soon meet and overlap across the adaxial surface of the leaf (fig. 1).

As the stipule increases in width, the walls laid down by the marginal row gradually become perpendicular to the surface of the stipule. This results in the production of a sheet of tissue one cell thick on both margins (fig. 15c). The apical row behaves in a similar manner, with the result that a complete border of tissue one cell thick is produced. At this stage the lateral portions of the young stipule consist of an outer fringe of tissue one layer of cells thick and an inner area two layers of cells thick, both of which are continuous from the base of one margin over the apex to the base of the other. Exactly the same description applies to a bud scale of *Morus* which has attained a height of  $750\mu$  or more. At maturity the margins of the stipule become scarious, and many of the marginal initials become the mother cells of unicellular hairs (fig. 15c). A type of marginal growth similar to that of the final phases of the bud scales and stipules of *Morus* has been described by Lund (1872) for the bud scales of *Taxus* and for the in-

volucral bracts of many composites. Lund's remarkable monograph, long unnoticed by students of foliar histogenesis, has recently been reviewed by Foster (1936).

The vascular supply of each stipule consists of a single small procambial strand which forms in the base of the organ and then differentiates acropetally and basipetally until a connection is established with the subtended lateral leaf trace. As the stipule increases in size additional procambial strands are formed. These differentiate acropetally and basipetally until they connect with the median strand. Occasionally isolated veinlets are formed which remain unconnected with other veins up to the time of bud expansion (figs. 16a, 16b). In stipules which have attained a height of  $1500\mu$  chloroplasts are sparingly formed in the peripheral cytoplasm of all cells except those of the epidermis (figs. 15a, 15b). In the thicker portions near the midrib, however, the chloroplasts develop much more abundantly near the abaxial surface, a situation quite in keeping with the fact that the stipules stand nearly erect with their abaxial surfaces exposed to stronger light.

Intercellular spaces are formed as the chlorophyll-containing cells enlarge and round off. The air spaces are continuous with the external atmosphere through stomata which are formed on the abaxial surface (figs. 13, 15a). The guard cells contain chloroplasts, but these are lacking in the rest of the epidermal system. A simple, uniform photosynthetic tissue is developed, with no differentiation into palisade and spongy mesophyll. The tissues of the stipules are relatively mature by the time the bud has reached its full size. This early maturation of the stipular tissues is in contrast to the very late maturation of the tissues of the foliage leaf. The relatively early maturation of the tissues of the bud scales and transition forms of *Carya* has been emphasized by Foster (1935a, 1935b), and possibly represents a characteristic feature of such organs.

The procambial strand in the median portion of the stipule matures rapidly into spiral xylem elements and very small phloem cells (figs. 14a, 15a). The vascular strand as seen in transection near the basal portion of the stipule is differentiated with two or three layers of cells intervening between it and the adaxial surface (fig. 14a). Sections higher up reveal that the strand is finally formed with the xylem abutting the adaxial epidermis (fig. 15a). Smaller veins and veinlets of from one to three xylem elements and a like number of parenchyma cells (figs. 14b, 15b) are found in the lateral portions of the maturing stipule. Unicellular, pointed hairs develop as extensions of the epidermal cells of the abaxial surface (fig. 12a). Later, similar hairs are sparingly formed on the adaxial surface (fig. 15a).

At the time of bud expansion the stipules elongate rapidly and finally

attain a length of about 8 mm. Growth in length is accomplished by the linear extension of the cells; and no cell divisions were found to occur



Figs. 16a-16b. Sketches of mature stipules showing variation in venation.  $\times 8\frac{1}{2}$ .

during elongation. The cells of a fully elongated stipule average about  $60\mu$  in length. The first function of the stipules is that of the protection of young axillary buds and inflorescences; but they soon expand and become photosynthetic organs. They fall from the twigs very early, before the adjacent foliage leaf has reached its full size. The abscission layer of each stipule extends laterally from the point of divergence of the stipule and petiole to the point of divergence of the leaf base from the stem.

The mature stipule is an oblong structure varying in thickness from about fifteen cells in the region of the midrib to one cell at the margin. Ordinarily one main vein, or midrib, is formed in the median portion (fig. 16b), continuous with which are differentiated numerous lateral veins and veinlets. The situation is quite variable, however, and frequently two or more veins of equal rank are found in place of a single midrib (fig. 16a).

#### DISCUSSION

A comparison of the modes of development of the bud scale, foliage leaf and stipule of *Morus alba* reveals several interesting points. The bud scale primordium appears at the side of the stem tip and grows directly, through the activity of definite apical and marginal meristems, to an adult bud scale. A homologous primordium is produced in connection with the origin of each foliage leaf and its associated stipules (fig. 2). This primordium, however, behaves in a manner entirely different from that of the bud scale. Growth suppression at two points, one on either side of its apex, results in the production of three foliar organs (the leaf and two stipules) which, at senescence, absciss independently. The leaf base becomes incorporated into the tissues of the node. From this behavior one might infer that the bud scale is, in a phylogenetic sense, a composite foliar structure consisting of a leaf base, a foliage leaf and two stipules. This is essentially the interpretation given by Henry (1846) for *Morus scabra*, and by Mikosch (1876) for *Tilia grandiflora*, although both of these workers spoke of

"fused" stipules and foliage leaf. A composite organ of this type could arise through the failure of the growth suppressions which normally bring about the separation of the stipules and foliage leaf, rather than by the fusion of these organs.

The bud scales and stipules of *Morus alba* exhibit many developmental similarities, and these may be listed as follows: 1) their mode of growth in width and length; 2) the rapidity with which the photosynthetic portions mature; 3) the absence of latex tubes; 4) the possession of but one type of stiff, pointed hairs; and 5) growth during bud expansion by the enlargement (not division) of cells. They differ markedly only with respect to the time of differentiation of their vascular supplies. The development of the foliage leaf contrasts with that of the bud scales and stipules in each of the above features. The corpus is involved to a greater extent in the origin of its primordium. It does not increase in length and width by means of single rows of initial cells. Its photosynthetic portions differentiate and mature relatively late, after the leaves have expanded from the bud. It has a well developed latex system which appears very early in the ontogeny of the midrib and petiole. It possesses two types of hairs which are distributed abundantly on the adaxial and abaxial surfaces. It grows during bud expansion by cell division.

These similarities between bud scales and stipules which contrast so strongly with features exhibited by the foliage leaf might lead one to the inference that the bud scale represents a leaf base and two fused stipules. A scale of this type could have arisen phylogenetically from a leaf base primordium by the failure of the normal growth suppressions which ordinarily produce the distinct primordia of foliage leaf and stipules, and by a complete failure of the foliage leaf to develop. However, interpretations based upon speculation of this type are difficult to prove, and in the past have led to considerable confusion.

The functions of the bud scales and stipules of *Morus* are dual ones, i.e. protection and photosynthesis (the latter to a limited extent). The function of the foliage leaf is exclusively photosynthetic. Similarities in function may lead, through natural selection or other means, to similarities in structure; and organs such as bud scales and stipules, which have similar functions, might be expected to exhibit similarities in structure. Structural similarities which may be based upon functional relationships are probably of little phylogenetic significance, and hence they should not be used in the interpretation of morphological data.

One might expect a bud scale derived by the fusion of two stipules and a foliage leaf, or by the fusion of two stipules alone to show histological features indicative of its composite nature. The bud scales of *Morus alba*

are very uniform in structure. There are no very prominent veins which might represent the midribs of the fused stipules and leaf, and there are no histogenetic features suggestive of a fusion of any kind. It is true that the scale and stipule are similar with respect to marginal and apical growth and in other ways, but this is not surprising in view of their similar function. It seems possible to the writer that the bud scale of *Morus* may have arisen phylogenetically from what is commonly regarded as the foliage leaf primordium, not by a fusion of the foliage leaf and stipules or by a fusion of stipules alone, but from a failure of the foliage leaf and stipules to differentiate at all. A structure derived in this manner can be regarded neither as a combination of foliage leaf and stipules, nor as a modification of these organs. It is a different kind of foliar organ, with a distinctive histogenetic development, and deserves to be recognized as such.

The most important function of the bud scale is that of protection, and it begins its duties very early in its ontogeny. Its rapid and economical methods of apical and marginal growth are in keeping respectively with its function and its lack of permanency. The rapid maturation of its tissues is readily correlated with the fact that it functions as a protective organ throughout its existence.

With respect to the contrasting views of Goebel (1932) and Foster (1935a) concerning the multipotence of foliar primordia, the writer feels that very little evidence can be obtained by histogenetic studies alone. In the case of *Morus alba* the primordia of bud scales and foliage leaves are not distinguishable with certainty up to the  $70\mu$  stage. This is not, however, equivalent to saying that they are identical. Goebel was able to produce by defoliation experiments involving certain woody types, branches upon which foliage leaves replaced the bud scales. This provides an interesting example of the plasticity of living tissues; but it is not convincing as evidence in favor of the theory that bud scales are "transformed" foliage leaves. Histogenetic studies show no evidence of an "arrest" or "transformation" in connection with the development of the bud scale; but proponents of the theory might readily take the view that these processes occur very early in ontogeny, and in a manner so subtle as to be undetectable by ordinary histological methods. The developmental morphologist can hope to record only an accurate account of the visible changes that occur when a foliar structure develops; he can provide very little evidence as to the ultimate nature of a structure.

The writer has long been puzzled by the stipular situation exhibited by *Morus* and other genera with free, lateral stipules. In *Morus* the stipular scars and foliage leaf scars are not contiguous, but are separated by appreciable nodal areas. Two interpretations of this situation are possible. If

the stipules are products or divergences of the base of the foliage leaf as suggested by Eichler (1861), abscission of the leaf must occur above the base, leaving the latter as a portion of the node. This interpretation, while of interest to the morphologist, is confusing to specialists in the other branches of plant science, who need a clarified terminology in their research. A second interpretation might be given, namely that the stipules are neither attached to, nor diverged from the leaf base at all, but are products of the closely adjacent cauline tissue which has diverged slightly at the node, in adjustment to leaf production. The diverged portion of the node might then be considered a leaf-stem transition region. As a step in the solution of the problem increased knowledge concerning the development of the node and the nodal appendages might prove helpful. We have a great fund of knowledge concerning the structure and development of stems, roots and root-stem transitional regions; but very little information concerning the development of the node, foliage leaves, stipules or bud scales is available.

#### SUMMARY

1. Both tunica and corpus are involved in the origin and development of the foliage leaf.

2. The primordium of the foliage leaf appears as a crescent-shaped structure to the side of the growing point of the stem. When the primordium is about  $70\mu$  in height three meristematic areas may be discerned near its apex. Two of these are lateral and represent the young stipules. The other is median and constitutes the primordium of the midrib of the foliage leaf.

3. The mode of development of the stipules differs greatly from that exhibited by the foliage leaf, but it is strikingly similar in all essential features to the development of the bud scales. The main points of similarity shown by stipules and bud scales are as follows: a) the structure and behavior of the apical and marginal meristems; b) the early maturation of tissues; c) the presence of but one type of epidermal hair; and d) the absence of a latex system. The foliage leaf differs from the bud scale and stipules in the following features: a) the structure and behavior of its apical and marginal meristems; b) the late maturation of its tissues; c) the presence of two types of epidermal hairs distributed on both surfaces; and d) the presence of a well developed latex system.

4. The histogenetic development of the stipule differs from that of the bud scale in one important particular, i.e., with respect to the time of differentiation of the procambium. In the case of the bud scale the procambium appears when a height of about  $750\mu$  has been attained. In the stipule



the procambium is detectable at a much earlier stage, when the organ is about  $70\mu$  high.

5. The similarities in development and structure of the bud scales and stipules are correlated with the similar functions of these structures. They are not accepted as evidence of homology.

6. It is suggested that the bud scale of *Morus alba* could have arisen phylogenetically from a primordium of the type exhibited by the modern foliage leaf, but that it represents an entirely divergent product of the primordium in which there is no differentiation of stipules and foliage leaf and no proved homologies with these organs.

7. Further studies on stipules and bud scales are needed before general morphological interpretations are attempted.

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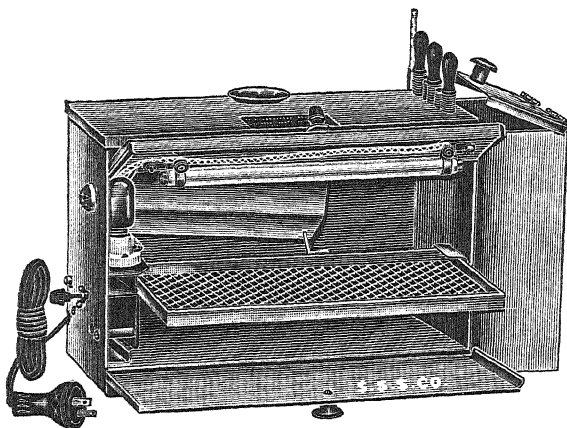
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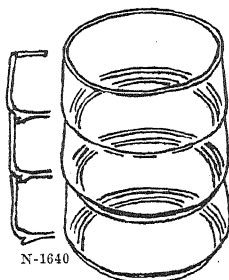
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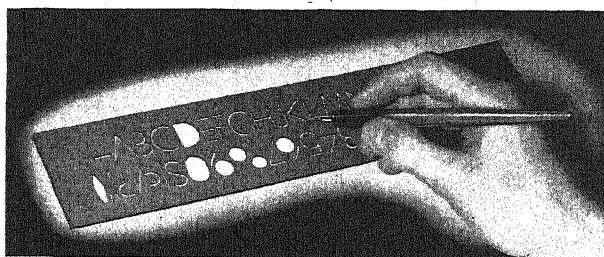
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## Salient lines of structural specialization in the wood parenchyma of dicotyledons

DAVID A. KRIBS<sup>1</sup>

(WITH PLATES 3 AND 4 AND ONE TEXT FIGURE)

The author in an initial paper (1927),<sup>2</sup> and in a subsequent paper (1930), endeavored to establish correlations between anatomical characters of the stem and morphological characters of the flowers, fruits, and leaves. Since 1927, a number of investigators have studied specific families from the same standpoint. As previously mentioned (Kribs, 1935), the results obtained thus far are more or less contradictory; high correlations frequently occur in groups of closely related species and genera, whereas, serious discrepancies arise in the case of large families and orders.

While taxonomists have taken into consideration lines of structural specialization of the flower in a supposedly natural system of classification, wood technologists, studying correlations between stems and flowers of specific families, have thus far, with the exception of Chattaway (1932) and Webber (1934), entirely ignored natural relationships from the standpoint of wood structure. From results obtained, I and other investigators have endeavored to show correlations between a natural system based on floral structure and an artificial system based on stem structure. When natural relationships are taken into consideration, there is much evidence to indicate that as the size of the unit of classification increases, the degree of correlation between structural specialization of stems and flowers becomes lower, and in some cases there is no correlation whatever, even in small groups. Unless the taxonomist feels inclined to further sub-divide the larger units, an independent natural system will ultimately have to be formulated for woods.

Bailey and Tupper (1918), and Bailey (1920, 1923), and Frost (1930) have shown that the salient lines of structural specialization in the cambium and tracheary elements of dicotyledons are so distinct and so closely correlated that they may be studied effectively by statistical methods. Their investigations demonstrate that the fusiform initials of the cambium and their derivatives are reduced in length as specialization increases.

The writer has endeavored to trace major lines of structural specialization in the wood rays and wood parenchyma of dicotyledons. The present

<sup>1</sup> National Research Council Fellow.

<sup>2</sup> This investigation was conducted at the University of Minnesota as partial fulfillment of a course in anatomy of vascular plants under the direction of Dr. F. K. Butters.



paper deals with wood parenchyma. Although the investigation was based on the study of 782 genera, because the writer was unable to collect sufficient material from families representing the various vasicentric types, he was unable to make a detailed study of these groups; therefore, the four highly specialized paratracheal parenchyma types, viz., *banded paratracheal*, (fig. 6), *abundant vasicentric*, (fig. 7), *confluent*, and *aliform*, (fig. 8), were grouped into one parenchyma type called *vasicentric abundant* in this investigation.

The *vasicentric abundant* parenchyma types as represented by figures 6, 7, 8, and 10 are all highly specialized but the question naturally arises, which of the four types is the most highly specialized? The problem is: as woods become more highly specialized, does the parenchyma increase or decrease in amount around the vessels? This can best be illustrated by examination of the accompanying photomicrographs. There are several possibilities: one sequence, from figure 6, *banded paratracheal*, to figure 10, *banded paratracheal* and *confluent*, to figure 8, *confluent*, *aliform* and *vasicentric*, to figure 7, *vasicentric*; A second sequence, from figure 7, *vasicentric*, to figure 8, *confluent*, *aliform*, and *vasicentric*, to figure 10, *banded paratracheal* and *confluent*, to figure 6, *banded paratracheal*.

The results of the present investigation show that in the metatracheal<sup>3</sup> parenchyma types woods become more highly specialized with an increase in the amount of parenchyma. One might naturally assume that, if this were true concerning metatracheal types, it would also be true concerning vasicentric types. Since wood parenchyma is fundamentally a storage tissue, one might infer, from a physiological viewpoint, that an increase in the amount of parenchyma would indicate specialization. On the other hand, the results of a number of investigations seem to show, in many instances, that reduction indicates specialization in both stems and flowers.

Upon receipt of additional material for study, the writer hopes to show, in a subsequent paper, the natural sequence within the vasicentric parenchyma types.<sup>4</sup>

#### METHODS

Methods similar to those used in the earlier paper (1935) were followed. The woods were divided into six groups upon the basis of the structure of their tracheary tissue, as follows: scalariform I, scalariform II, scalariform-porous, porous-oblique, porous-oblique and transverse, and porous-transverse. The wood parenchyma types were then studied in detail for each group separately.

<sup>3</sup> The meaning of the term metatracheal in this case is synonymous with non-paratracheal.

<sup>4</sup> The writer is particularly desirous of obtaining from other investigators hand specimens of as many as possible of the woods which possess paratracheal parenchyma.

## DISCUSSION

According to the latest publication by the Committee on Nomenclature, International Association of Wood Anatomists (1933), the following types of wood parenchyma are recognized:

1. *Diffuse parenchyma*.—Single parenchyma strands or cells distributed irregularly among the fibrous elements of the wood, as seen on cross section (fig. 1).

2. *Terminal parenchyma*.—Aggregated wood parenchyma forming a more or less continuous layer of variable width at the close of the season's growth (fig. 5).

3. *Metatracheal parenchyma*.—Aggregated wood parenchyma forming concentric laminae, mostly independent of the vessels and vascular tracheids (figs. 3 and 4).

4. *Paratracheal parenchyma*.—Aggregated wood parenchyma in association with the vessels or vascular tracheids (figs. 6, 7, 8, 9, 10).

5. *Vasicentric parenchyma*.—Paratracheal parenchyma forming a vascular sheath of variable width, and circular or oval in cross section (fig. 7).

6. *Aliform parenchyma*.—Vasicentric parenchyma with wing-like lateral extensions (fig. 8).

7. *Confluent parenchyma*.—Coalesced aliform parenchyma, forming irregular tangential or diagonal bands (figs. 8, 10).

The writer wishes to add to this list two additional parenchyma types, numbers 8 and 9 immediately following, which are constant structures in many woods.

8. *Diffuse-aggregate parenchyma*.—A mixture of diffuse parenchyma and parenchyma in short tangential arcs two to ten cells long (fig. 2).

9. *Banded paratracheal parenchyma*.—Paratracheal parenchyma in wide tangential bands (fig. 6).

Table 1 shows the percentage of wood parenchyma types in each vessel type. Scalariform 1 represents the most primitive type of vessel element; porous-transverse, the most highly specialized type. There is a high correlation between parenchyma type and vessel element type. *Diffuse* parenchyma predominates in the stems with the scalariform type of vessel element. *Diffuse-aggregate* and *vasicentric scanty* parenchyma predominate in the scalariform-porous and porous-oblique vessel element types. *Metatracheal narrow* parenchyma reaches its highest development in the porous-oblique and transverse group. *Metatracheal wide* parenchyma occurs only in the porous-oblique and transverse and the porous-transverse groups, while *vasicentric abundant* parenchyma is very conspicuous in the porous-transverse group.

Reading across the table in each vessel element group, *diffuse* and

TABLE 1  
*Percentage of parenchyma types in each vessel type*

TYPE OF VESSEL ELEMENT	NUMBER OF GENERA	PARENCHYMA TYPES							
		DIFFUSE	DIFFUSE AGGREGATE	VASI- CENTRIC SCANTY	METATRA- CHEAL NARROW	METATRA- CHEAL WIDE	VASI- CENTRIC ABUNDANT	PAREN- CHYMA ABSENT	TER- MINAL
Scalariform I	63	69.84	19.04					11.12	
Scalariform II	32	59.37	15.62					12.50	12.51
Scalariform-porous	68	13.23	41.18	20.59	8.82			11.76	4.42
Porous-oblique	202	11.88	32.65	15.78	8.41		11.96	12.87	6.45
Porous-oblique and transverse	192	4.16	14.06	7.81	17.18	10.42	31.28	4.16	10.93
Porous-transverse	225		2.69		6.66	9.33	70.22	1.77	9.33

*diffuse-aggregate* parenchyma are the only types which occur in the woods with the scalariform I vessel elements. *Diffuse* parenchyma constitutes nearly 70 per cent of the parenchyma types in the scalariform I group, and nearly 60 per cent in the scalariform II group. In the scalariform-porous group, *diffuse-aggregate* and *vasicentric scanty* parenchyma constitute nearly 62 per cent of the total parenchyma types, 41 per cent being of the *diffuse-aggregate* type. *Diffuse-aggregate* and *vasicentric scanty* parenchyma are also dominant in the porous-oblique group, making up 48 per cent of the total parenchyma types. In the porous-oblique and transverse group, the *metatracheal* and *vasicentric abundant* parenchyma types predominate and are of almost equal importance, 27 per cent being *metatracheal* and 31 per cent *vasicentric abundant*; while in the porous-transverse group, 70 per cent of the parenchyma types is *vasicentric abundant*.

Table 1 shows rather conclusively that the *diffuse* condition is indeed the primitive type of parenchyma distribution, and that *vasicentric abundant* represents the most highly specialized type. *Diffuse-aggregate*, *vasicentric scanty*, *metatracheal narrow*, and *metatracheal wide* represent transitional types, the evolutionary sequence being in the order named. The *vasicentric scanty* type is apparently an offshoot of the *diffuse-aggregate* condition, but it is a question as to whether it passes directly to the *vasicentric abundant* type by an accumulation of parenchyma around the vessels, or whether it passes first through the transitional *metatracheal* types.

Table 1 and corroborative data in table 2 show that in arborescent dicotyledons an absence of wood parenchyma indicates a primitive condition. In addition, table 1 shows that there is no correlation between vessel element type and *terminal* parenchyma distribution. *Terminal* parenchyma occurs as an offshoot in practically every type of woody dicoty-

TABLE 2  
Average length of vessel element in mm. for each parenchyma type\*

TYPE OF PARENCHYMA	NUMBER OF GENERA	AVERAGE ELEMENT LENGTH (MM.)
Diffuse	104	.92
Absent	57	.78
Diffuse-aggregate	144	.65
Vasicentric scanty	61	.60
Metatracheal narrow	71	.51
Terminal	62	.44
Metatracheal wide	41	.42
Vasicentric abundant	242	.31

\* Vessel element length indicates total length, tip to tip, from macerated material.

ledonous stem indicating that it is a specialization due to reduction. This viewpoint is further substantiated by data in tables 2 and 3 and is in harmony with Jeffrey's statement (1917) that "terminal parenchyma is accordingly a phenomenon of reduction in the dicotyledonous series."

Table 2 shows a high correlation between parenchyma type and vessel element length and corroborates the data in table 1 in that *diffuse* parenchyma is the primitive type and that as woods become more highly specialized they pass through the transitional *diffuse-aggregate*, *vasicentric scanty*, and *metatracheal* types, and finally culminate in the highly specialized *vasicentric abundant* types. Figure 11 illustrates diagrammatically the salient lines of structural specialization in the wood parenchyma of dicotyledons.

TABLE 3  
Average width and length of parenchyma cells in mm. for each parenchyma type

TYPE OF PARENCHYMA	AVERAGE WIDTH OF PARENCHYMA CELL IN MM.	AVERAGE LENGTH OF PARENCHYMA CELL IN MM.	RATIO OF LENGTH TO WIDTH
Diffuse	.0095	.154	16.21
Diffuse-aggregate	.017	.121	7.11
Vasicentric scanty	.0195	.110	5.64
Metatracheal narrow	.020	.102	5.10
Terminal	.020	.090	4.50
Metatracheal wide	.0275	.095	3.45
Vasicentric abundant	.028	.088	3.14

Table 3 shows that as woods become more highly specialized, the individual parenchyma cell parallels the development of the vessel element in that it becomes shorter and wider.

#### SUMMARY

1. There is a high correlation between vessel type and wood parenchyma type; the evolutionary sequence being from the diffuse parenchyma

type, the most primitive, through the transitional diffuse-aggregate, vasicentric scanty, and metatracheal types, to the highly specialized vasicentric abundant types.

2. An absence of wood parenchyma indicates a primitive condition.

3. Terminal parenchyma is a specialization due to reduction.

4. As woods become more highly specialized, the individual parenchyma cell parallels the development of the vessel element in that it becomes shorter and wider.

The writer expresses his thanks to the National Research Council for the grant which made this investigation possible, and to Professor I. W. Bailey for his continued advice and criticism.

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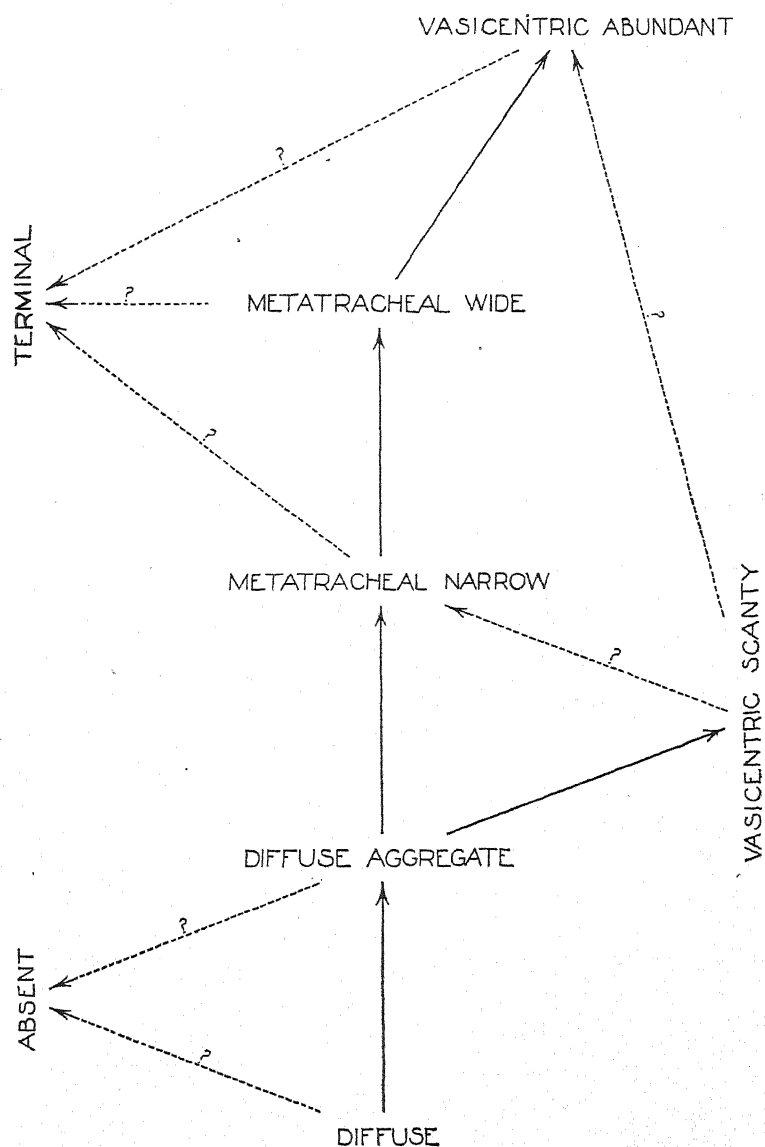


Fig. 11. Diagrammatic illustration of salient lines of structural specialization in the wood parenchyma of dicotyledons.

## Description of plates

## Plate 3

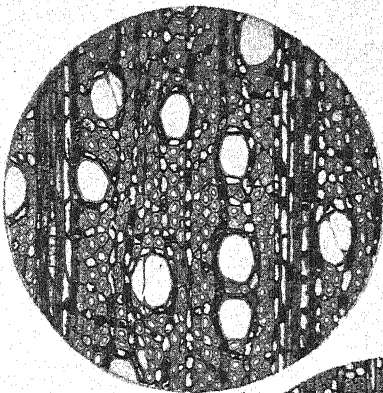
Fig. 1. *Ternstroemia cooalis* A. Rich. Transverse section of the xylem, illustrating *diffuse* wood parenchyma.  $\times 74$ .

Fig. 2. *Myrocarpus simplicifolius* Brong. & Gr. Transverse section of the xylem, illustrating *diffuse-aggregate* wood parenchyma.  $\times 74$ .

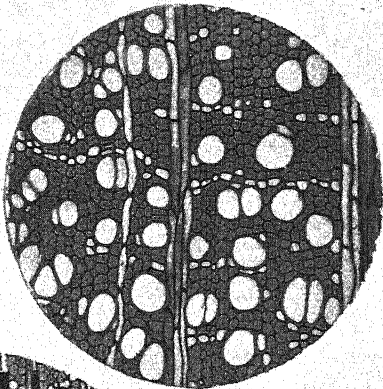
Fig. 3. *Eschweilera laevifolia* Miers. Transverse section of the xylem, illustrating narrow *metatracheal* wood parenchyma.  $\times 74$ .

Fig. 4. *Kayea paniculata* Merr. Transverse section of the xylem, illustrating wide *metatracheal* wood parenchyma.  $\times 74$ .

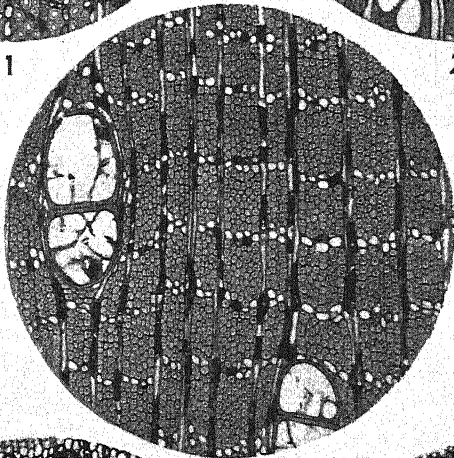
Fig. 5. *Osmanthus americanus* (L) Benth. & Hook. Transverse section of the xylem, illustrating *terminal* wood parenchyma.  $\times 74$ .



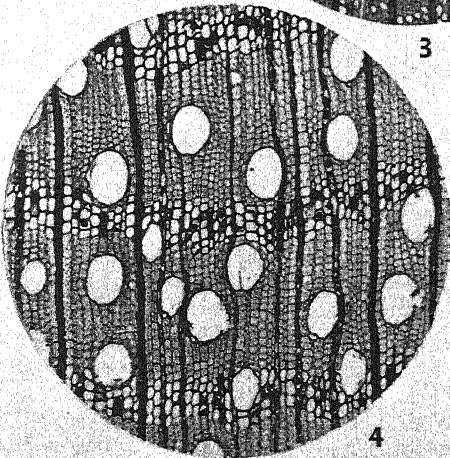
1



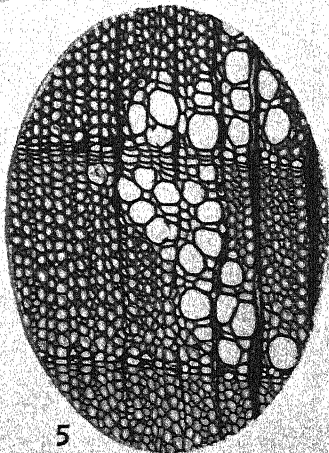
2



3



4



5



## Plate 4

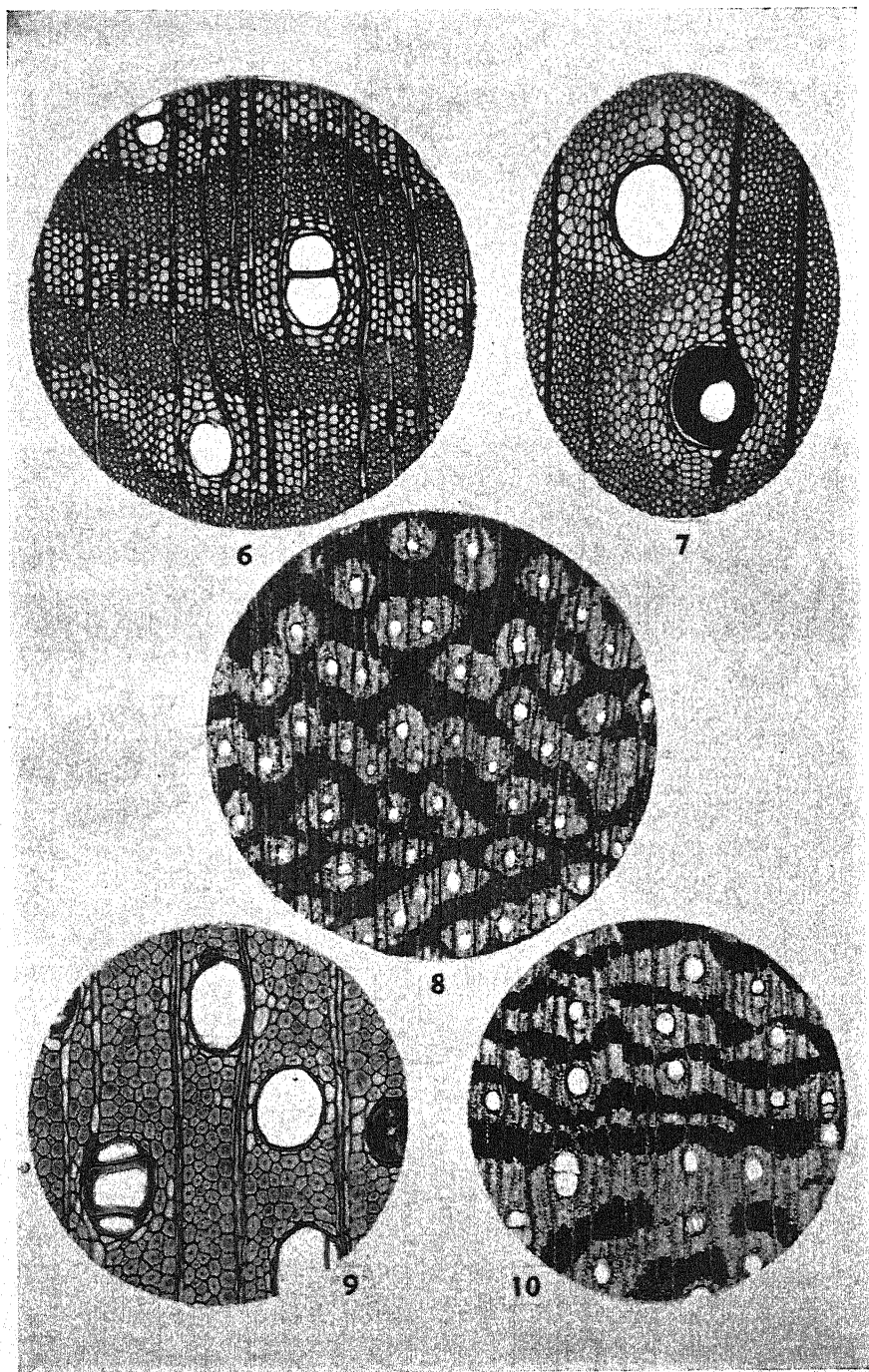
Fig. 6. *Bauhinia* species. Transverse section of the xylem, illustrating *banded paratracheal* wood parenchyma.  $\times 74$ .

Fig. 7. *Albizzia procera* Benth. Transverse section of the xylem, illustrating abundant *vasicentric* wood parenchyma.  $\times 74$ .

Fig. 8. Tropical legume. Transverse section of the xylem, illustrating wood parenchyma of mixed *confluent*, *aliform*, and *vasicentric* types.  $\times 15$ .

Fig. 9. *Urandra corniculata* Foxw. Transverse section of the xylem, illustrating scanty *vasicentric* wood parenchyma.  $\times 74$ .

Fig. 10. *Andira* species. Transverse section of the xylem, illustrating *banded paratracheal* and *confluent* wood parenchyma.  $\times 17$ .





## Notes on the cytology and distribution of the Dioscoreaceae

BEN W. SMITH

(WITH TWO FIGURES)

In recent years plant cytologists have begun to investigate the chromosomal configurations of dioecious angiosperms in an effort to interpret the determination of sexual phenomena in the higher plants. Meurman (1925) and Lindsay (1930) have published lists of dioecious species in which heterochromosomes have been observed. In most cases the heteromorphic elements which occur in these plants have been thought to be sex chromosomes similar to those found in animals.

In the present paper heterochromosomes are reported from several species of *Dioscorea* in which the mitotic divisions of the root tips have been studied. During the brief course of this investigation it has not been possible to examine the meiotic divisions of the various species, but the results at hand are now summarized pending additional study.

### TAXONOMY AND DISTRIBUTION OF THE DIOSCOREACEAE

The family Dioscoreaceae is a natural group of tuber-forming, tropical vines. This family is usually allied with the Liliales and placed near the Amaryllidaceae. Members of the family have been a classic subject for morphological study, for a number of anomalous structures occur which have made it difficult to place this family in the phylogeny of the angiosperms. The tubers of the principal genus, *Dioscorea*, have great economic value in the tropics, where they are one of the chief starchy foods. The cultural history of the genus in the Eastern Hemisphere has been discussed by Burkill (1924). A striking feature of the cultivated species is the multiplicity of varietal types, many of which are relatively ancient in origin. As in some of these species one of the sex forms is unknown, it is evident that vegetative reproduction has played a very important part in the more recent evolution of the dioscoreas.

The family is divided into two tribes: the Dioscoreae, including six genera all of which have unisexual flowers, and the Stenomeridae with three genera which produce hermaphroditic flowers. The genus *Dioscorea* is by far the largest group, including about 90% of the species and distributed throughout the region in which any representatives of the family are found. A survey of the distribution of the family was made in connection with the present work. It has been based upon a recent monograph of the Dioscoreaceae Knuth, (1924) and the compilation of the *Index Kewensis* (Hooker and Jackson, 1886-1930). The systematic ar-

rangement of Knuth (1924), with the number of species and the distribution given in his work is presented in table 1.

TABLE 1  
*Classification and distribution of the Dioscoreaceae*

	NO. SPECIES	DISTRIBUTION
Tribe I. Dioscoreae		
1. <i>Dioscorea</i> L.	ca. 620	All tropical regions; a very few in temperate Europe and North America
2. <i>Higinbothamia</i> Uline	1	Yucatan (Cent. Am.)
3. <i>Boderea</i> Miegl.	1	Pyrenees Mts. (Europe)
4. <i>Epipetrum</i> Phil.	3	Chile
5. <i>Rajania</i> L.	24	West Indies
6. <i>Tamus</i> L.	4	Europe and North Africa
Tribe II. Stenomeridae		
7. <i>Stenomeris</i> Planch.	5	East Indies
8. <i>Trichopus</i> Gaertn.	1	Southern India, Ceylon
9. <i>Petermannia</i> F. Muell.	1	New South Wales (Australia)
Total species	ca. 660	

Knuth has included about 620 species in the genus *Dioscorea* while the *Index Kewensis* lists about 840 species in the genus. The disparity in numbers is explained by the method of compilation employed in the *Index Kewensis* which has accepted species in the earlier volumes and later has reduced these names to synonyms. In this work the original description is cited and the distribution is given. Since the distribution is taken from the original description of the species, it is often unduly limited. Table 2 is condensed to indicate the general regions of the world from which the species have been described.

TABLE 2  
*General geographical distribution of the genus Dioscorea*

	NO. SPECIES
Western Hemisphere	
North America (excluding Mexico)	9
West Indies	15
Mexico and Central America	74
South America	354
Total	452
Eastern Hemisphere	
Europe and Asia Minor	3
Africa (including Madagascar)	147
Asia Continent	103
Japan, Formosa, Hongkong, Philippines	44
East Indies, Australia, Oceania	77
Total	374
Distribution indeterminate or unknown	16
Total described species in the genus	842

About half of the described species of *Dioscorea* are found in Central and South America, and most of the remainder are distributed over tropical Africa, Asia and the East Indies. The more commonly cultivated species, *D. alata*, *D. esculenta* and *D. bulbifera* have been widely disseminated and occur through most of the tropical range of the genus. The two former species are unknown outside of cultivation. In contrast to the cosmopolitan domesticated members of the genus, a large number of the wild species are indigenous to small areas.

#### THE CYTOLOGICAL PROBLEM

Only four authors have previously considered the chromosomes of any members of the Dioscoreaceae. An unnamed *Dioscorea* species was included by Strasburger (1909) in an investigation of pollen formation in various phanerogamous plants. Suessenguth (1921) studied the nuclear divisions of *D. sinuata* Vell. in meiosis and mitosis. He recorded the presence of 20–25 prochromosomes in root tip nuclei and reported the metaphase chromosome number to be  $2n=24$ . This count was corrected by Meurman (1925) who figured an anaphase of the first meiotic division of *D. sinuata* in which one plate had  $n=17$ , while the other showed  $n=17+1$ . This was reported as a case of the *Protenor* or XO type of sex chromosomes. Meurman determined the  $n$  numbers of two other species from pollen mother-cell divisions. The  $2n$  chromosome numbers of four species of *Dioscorea* were reported by Nakajima (1934).

Table 3 summarizes the chromosome counts which appear in the literature.

TABLE 3

*Chromosome numbers of Dioscorea and Tamus determined by previous investigations*

SPECIES	$n$ NUMBER	$2n$ NUMBER	AUTHOR
<i>Dioscorea batatas</i> Decne.		male, ca. 140	Nakajima, 1934
<i>D. caucasica</i> Lipsky	male, 10		Meurman, 1925
<i>D. japonica</i> Thunb.		male, 40	Nakajima, 1934
<i>D. sinuata</i> Vell.	male, 17 female, 18	ca. 35	Meurman, 1925
<i>D. tokoro</i> Makino		male, 20	Nakajima, 1934
<i>D. gracillima</i> Miq.		male, 20 female, 20	Nakajima, 1934
<i>Tamus communis</i> L.	male, 24		Meurman, 1925

The present study was undertaken for the purpose of investigating any obtainable species of the genus *Dioscorea*, with special reference to the probable occurrence of sex chromosomes in these dioecious plants.

#### MATERIAL AND METHODS

Several strains of *Dioscorea villosa* L. were collected near Charlottesville, Virginia, in the Shenandoah National Park, and in Clarke County,

Virginia. Aerial tubers of *D. batatas* Decne. (introduced) were obtained from cultivated plants in Charlottesville and Front Royal, Virginia. In addition over fifty strains including about twenty-five species were received from various botanic gardens of America and Europe and from the Division of Plant Exploration and Introduction of the United States Department of Agriculture.

Although most of the plants grew rapidly, none of them flowered before the first killing frost. For this reason buds were not obtained for the study of meiotic divisions, nor was it possible to check the identification of the species received. In each case the name of the species has been listed as it was sent with the material and this is followed by the source. All of the plants or seed were received during the spring of 1935.

At intervals during the 1935 growing season root tips were fixed in Nawaschin's chrom-acetic-formol plant fixative (Sax, 1931) and imbedded in paraffin. This material was sectioned at 10 to 12 microns and stained in crystal violet with picric acid as a counter stain (Smith, 1934). This method was found to be more satisfactory than Heidenhain's haematoxylin or the aceto-carmin smear technic.

#### OBSERVATIONS

The diploid chromosome numbers of thirteen species of *Dioscorea*, which have been determined by a study of somatic division figures in the root tips, are listed in table 4.

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#### Explanation of figures

Drawings were made with a Zeiss camera lucida in combination with Zeiss 90 $\times$  and 100 $\times$  achromatic objectives and a 30 $\times$  compensating ocular. Figures 1A, 1F, 2A, and 2D were drawn at a magnification of 4600; the other plates were drawn at 5000.

#### Figure 1

- A. Metaphase chromosome complement of *Dioscorea batatas* Decne. from Charlottesville, Va. ( $2n=144$ ).
- B. Metaphase of *D. cayenensis* from Palermo ( $2n=140$ ).
- C. Metaphase of *D. pentaphylla* L. from Zagreb ( $2n=144$ ).
- D. Metaphase of *D. oppositifolia* from Palermo ( $2n=140$ ).
- E. Metaphase of *D. caucasica* Lipsky from Berlin-Dahlem ( $2n=20$ ).
- F. Metaphase of *D. quinqueloba* Thunberg from Königsberg ( $2n=20$ ).
- G. Metaphase of *D. macroura* Harms. from Greitswald ( $2n=40$ ).
- H. Metaphase of *D. discolor* from Greitswald ( $2n=40$ ).
- I. Metaphase of *D. fargesii* Franch. which does not show associations, from Frankfurt-am-Main ( $2n=64$ ).
- J. Metaphase of *D. fargesii* showing typical association ( $2n=64$ ).

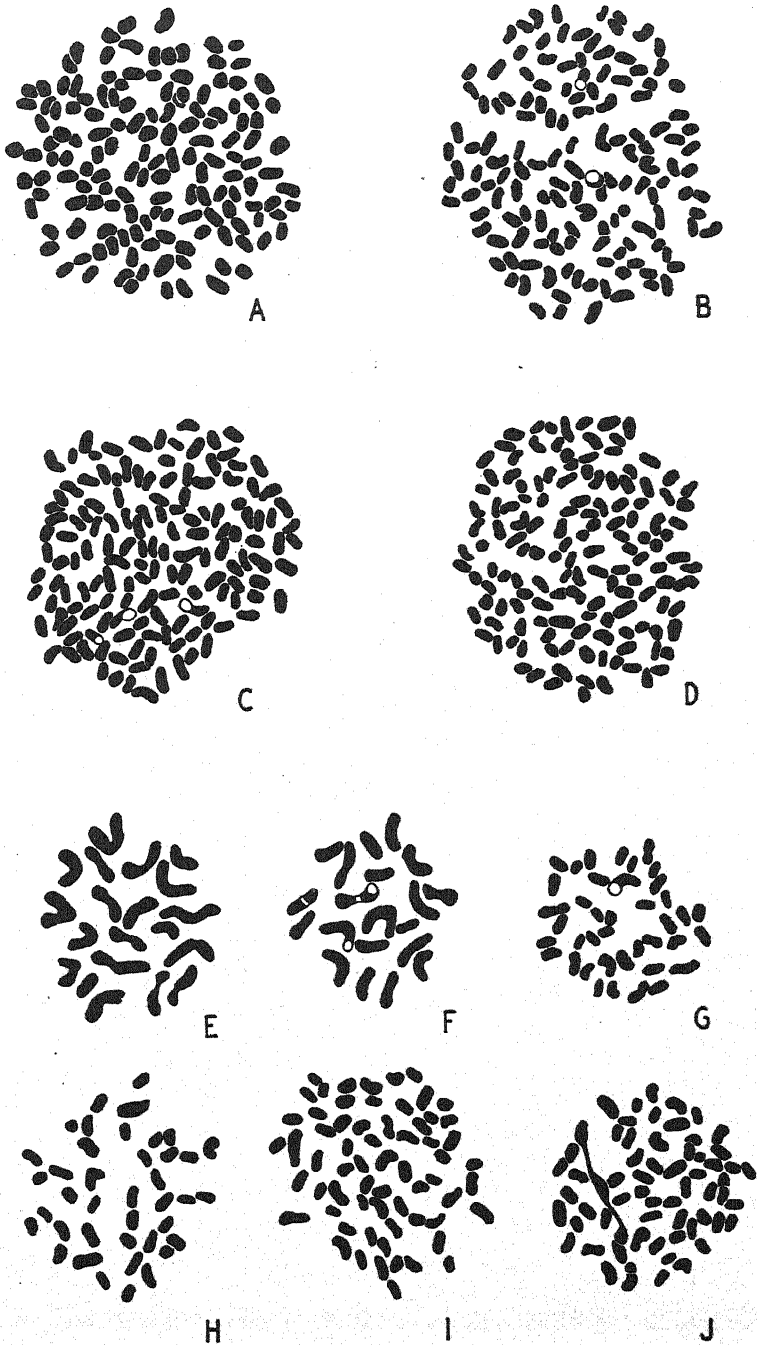


Figure 1 (See opposite page for explanation)



TABLE 4

*Chromosome numbers of Dioscorea determined in the present investigation*

STRAIN NO.	SPECIES NAME	2n NUMBER	SOURCE
1	<i>D. villosa</i> L.	ca. 60	Monticello Mt., Albemarle Co., Va.
2	<i>D. batatas</i> Decne.	ca. 144	Charlottesville, Va.
5	<i>D. alata</i> L.	ca. 81	U. S. D. A. F. P. I. #93492
9	<i>Dioscorea</i> sp.	ca. 40	U. S. D. A. F. P. I. #61308
11	<i>Dioscorea</i> sp.	ca. 40	U. S. D. A. F. P. I. #69077
15	<i>D. bulbifera</i>	80	Royal Botanic Garden, Edinburgh
18	<i>D. caucasica</i> Lipsky	20	Regio Institute e Orto Botanica, Roma
20	<i>D. caucasica</i> Lipsky	20	Botanischer Garten, Berlin-Dahlem
21	<i>D. caucasica</i> Lipsky	20	Zagreb
22	<i>D. cayenensis</i>	ca. 140	Palermo
25	<i>D. discolor</i>	40	Botanischer Garten, Greitswald
28	<i>D. fargesii</i> Franch	64	Palmengarten, Frankfurt-am-Main
38	<i>D. macroura</i> Harms.	40	Botanischer Garten, Greitswald
40	<i>D. oppositifolia</i>	ca. 140	Palermo
41	<i>D. pentaphylla</i> L.	ca. 144	Zagreb
42	<i>D. quinqueloba</i> Thunb.	20	Botanischer Garten der Univ. Königsberg
44	<i>D. reticulata</i> C. Gay	ca. 61	Palermo

(All plants received in the spring of 1935)

Four species, *D. batatas*, *D. cayenensis*, *D. oppositifolia* and *D. pentaphylla*, have  $2n = 140$  or  $144$  chromosomes. The plants which were grown could not be distinguished by their vegetative characters and may belong to the same species, although they were received under different names. The counts are taken from plates such as those shown in Figure 1A-1D.

Three strains of *D. caucasica* Lipsky were counted, and all had  $2n = 20$  chromosomes. In figure 1E the typical metaphase chromosomes of this plant are shown. Another species with the somatic number  $2n = 20$  is *D. quinqueloba* Thunb. In this species two chromosomes are known to have submedian constrictions (fig. 1F). Only a few chromosomes of all the plates studied showed definite constrictions. Most of these were seen in the species with relatively low numbers and larger chromosomes.

*D. alata* and *D. reticulata* C. Gay (Knuth, 1924, considers this name a synonym for *D. brachybotrya* var. *reticulata* Uline) are reported as having  $2n = 81$  and  $2n = 61$ , respectively. These counts have not been checked in the haploid condition, but the presence of the *Protenor* or XO type of sex chromosome is indicated (fig. 2B and fig. 2A).

The division figures of several other species showed evidence of morphologically distinct sex elements. These heterochromosomes occur in the plates of *D. macroura* and *D. discolor* in figures 1G and 1H. In each of these somatic complements it is possible to identify one element which is much larger than any of the other chromosomes. In the drawing of *D. reticulata* (fig. 2A) the extra chromosome is probably the element marked by

an x, since this chromosome is larger than the others and often has a definite ring shape as in this plate.

Associations of from three to five elements were usually present in the somatic metaphase plates of *D. fargesii* (figs. 1J and 2E). In some cases the association was not distinguishable (fig. 1I). The chromosome number

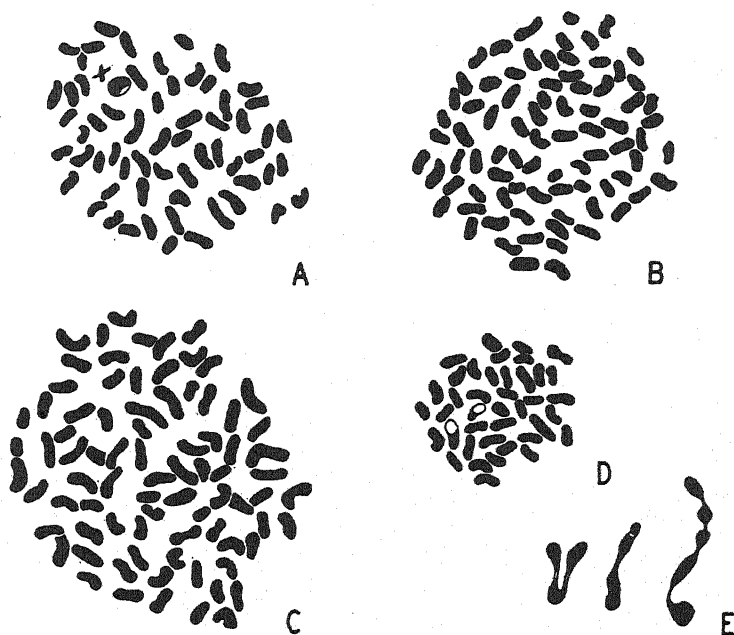


Figure 2

- A. Metaphase of *D. reticulata* Gay from Frankfurt-am-Main ( $2n=61$ ).
- B. Metaphase of *D. alata* L. from U. S. Dept. of Agriculture, F. P. I. #93492 ( $2n=81$ ).
- C. Metaphase of *D. bulbifera* from Edinburgh ( $2n=80$ ).
- D. Metaphase of unidentified *Dioscorea* sp. F. H. B. #61308, from U. S. Dept. of Agriculture ( $2n=40$ ).
- E. Chromosome associations from somatic plates of *D. fargesii*.

for this species is  $2n=64$ ; each element in the association was counted as one chromosome. Final interpretation was not attempted in the absence of meiotic material.

Prochromosomes were observed in the resting nuclei of all species. These chromatic bodies were peripheral as described by Manton (1935) for *Iberis* and *Biscutella* in the Cruciferae. The nuclei of *Dioscorea* contain the characteristic small chromosomes and single, large nucleolus of

Manton's "vesicular type." No prochromosome counts were attempted, but these bodies were much more numerous in the species which have the the higher numbered metaphase complements.

#### DISCUSSION

The chromosome numbers now known for the genus *Dioscorea* indicate that  $n=10$  is a basic number for this group. Of the seventeen numbers reported in the genus only four species have diploid numbers which are not multiples of 10. Two of the aberrant species, *D. sinuata* ( $2n=\text{ca. } 35$ ) and *D. fargesii* ( $2n=64$ ) have heterogeneous elements in their somatic chromosome complements which may be associated with sex determination. *D. pentaphylla* and *D. batatas* are reported as having  $2n=144$  but the large number of small chromosomes present in these species makes the accuracy of the determinations somewhat doubtful.

When the prevalence of vegetative reproduction in *Dioscorea* is considered, such a polyploid series as that described above is to be expected. It is known that many species in the genus are highly variable in their vegetative characters and much of this variability probably results from bud mutation. The evidence that is presented in this paper indicates that some of the mutations occurring in the dioscoreas are chromosomal rather than genic.

The bearing that the present observations may have upon the question of sex determination in dioecious plants is more obscure. Heteromorphic chromosomes undoubtedly occur in several *Dioscorea* species, but no conclusive data are now available for making final interpretations. A study of the meiotic behavior, correlated with the inheritance of the various degrees of intersexuality which occur in *Dioscorea*, is needed to establish relationships between these chromosomes and the sexual phenomena in the genus.

#### SUMMARY

1. The Dioscoreaceae is a natural family of tropical vines characterized by tubers, mostly unisexual flowers, and a range which includes the moist tropics of the world. The genus *Dioscorea* includes the cultivated yams of the tropics.

2. *Dioscorea* is the principal genus and includes 620 species of the 660 known in the family. The eight small genera have arisen from this ancestral group in various parts of the world and are, with one exception, very restricted in range.

3. The chromosome numbers of eighteen species of the Dioscoreaceae are known. Eleven of these are reported for the first time and camera lucida drawings are included in the figures.

4. Chromosome numbers in *Dioscorea* range from  $2n=20$ , in *D. caucasica*, to  $2n=144$ , in *D. batatas* and *D. pentaphylla*.

5. There is evidence to support the view that 10 is the basic chromosome number of the genus *Dioscorea*, for only four of the seventeen species counted have  $2n$  numbers which do not fall into a regular 10 series. Two of the aberrant numbers are in doubt and the other two involve heterochromosomes.

6. The heterochromosomes found in the division figures of *D. macroura*, *D. discolor*, *D. fargesii*, *D. reticulata*, and *D. alata* are identified as sex chromosomes pending an investigation of the meiotic divisions in these species. *D. reticulata* and *D. alata* have chromosome numbers of  $2n-1$  and are classed with *D. sinuata* Vell., examined by Meurman (1925), as belonging to the *Protenor* (XO) type.

7. Prochromosomes are reported from all of the species studied. The nuclei are of Manton's (1935) vesicular type with a single large nucleolus and prochromosomes arranged about the periphery of the resting nucleus.

The writer wishes to express his appreciation for the helpful advice and criticism of Professor Orland E. White, Director of the Blandy Experimental Farm, who has also generously assisted by procuring the material.

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UNIVERSITY OF VIRGINIA

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# A quantitative and ecological study of the larger aquatic plants of Sweeney Lake, Oneida County, Wisconsin<sup>1</sup>

L. R. WILSON

(WITH TWO FIGURES)

During the last six years considerable attention has been paid to the distribution and ecology of the larger aquatic vegetation in the lake region of northeastern Wisconsin. The present paper is the result of seven weeks intensive study during the summer of 1934 and numerous observations made during July and August in 1935.

These investigations have been carried out in connection with the limnobiological studies of the Wisconsin Geological and Natural History Survey with the intention of determining the floral and faunal productivity of various types of lakes. Sweeney Lake not only illustrates a lake type characteristic of the Northern Highland Region of Wisconsin, but recently it has been chosen by the Conservation Commission as a rearing pond for "wall-eyed" pike. For these reasons Sweeney Lake was studied.

This lake is located in the northern part of Oneida County in Sections 14, 15, 22, and 23, Township 39 North, and Range 7 East. It covers an area of 634,620 square meters and has a maximum depth of 5.7 meters (fig. 1).

## GEOLOGY AND WATER CHARACTERISTICS

The area in which Sweeney Lake is developed is very rugged. The topography is morainic and the drift is that of the Mankato Substage of the Wisconsin Stage of glaciation. The soils are largely of sand and gravel and show some evidence of assortment. Large boulders are frequent and several are found along the shore and in the shallow parts of the lake. Kettles are numerous and most of the smaller ones contain no water or evidence of ever having had any, but practically all of the larger kettle holes contain either peat deposits or lakes in various stages of development.

The basin of Sweeney Lake was formed with the melting of a buried or partially buried ice mass in the moraine.

The shores are mostly steep and opposite these, small wave cut beaches exist. Low places in the shoreline are to be found at Stations 5 and 18 as well as at the inlets and outlet.

<sup>1</sup> From the Limnological Laboratory of the Wisconsin Geological and Natural History Survey and Coe College. Report No. 63.

Two inlets at the southwest end of the lake supply sufficient water to keep the level of the lake constant even in years of little precipitation. The outlet, like the larger inlet, is a stream eight to ten meters wide and nearly one-half meter deep. There is a strong outflow of water. A small fish dam has been built across the outlet and this further insures the constancy of the water level in the lake.

The lake soils below the one meter level, are mostly of the well decomposed organic type, while above that depth they are usually sandy, or rocky. The sandy soils are often mixed with chips and larger pieces of wood. The abundance of wood in the soils can probably be attributed to the comparatively recent lumbering operations in this region. In the bays (Stations 5, 14 and 18) the organic soils reach the shores and at these points bogs are encroaching upon the water. In the bay containing the inlets (Station 14) the organic soils are much less decomposed than in the other bays. This is due to the deposition of such materials at the mouths of the inlets. The larger stream flows through bog land and the coarse organic materials originate there.

The abundance of the organic soils in the shallow water indicates that Sweeney Lake is in a mature stage of lake development.

The fact that the lake is part of a drainage system would suggest that its water would be at least medium hard. This is borne out by chemical analysis, for the bound carbon dioxide content was found to be 18.25 parts per million, the conductivity, 60, and the pH 8.2. Physical observations upon the water indicate that its color is 52 at the surface, and a six inch white disc was visible only to a depth of .6 of a meter on August 25, 1929. The water is usually very turbid. This is due largely to the abundance of phytoplankton.

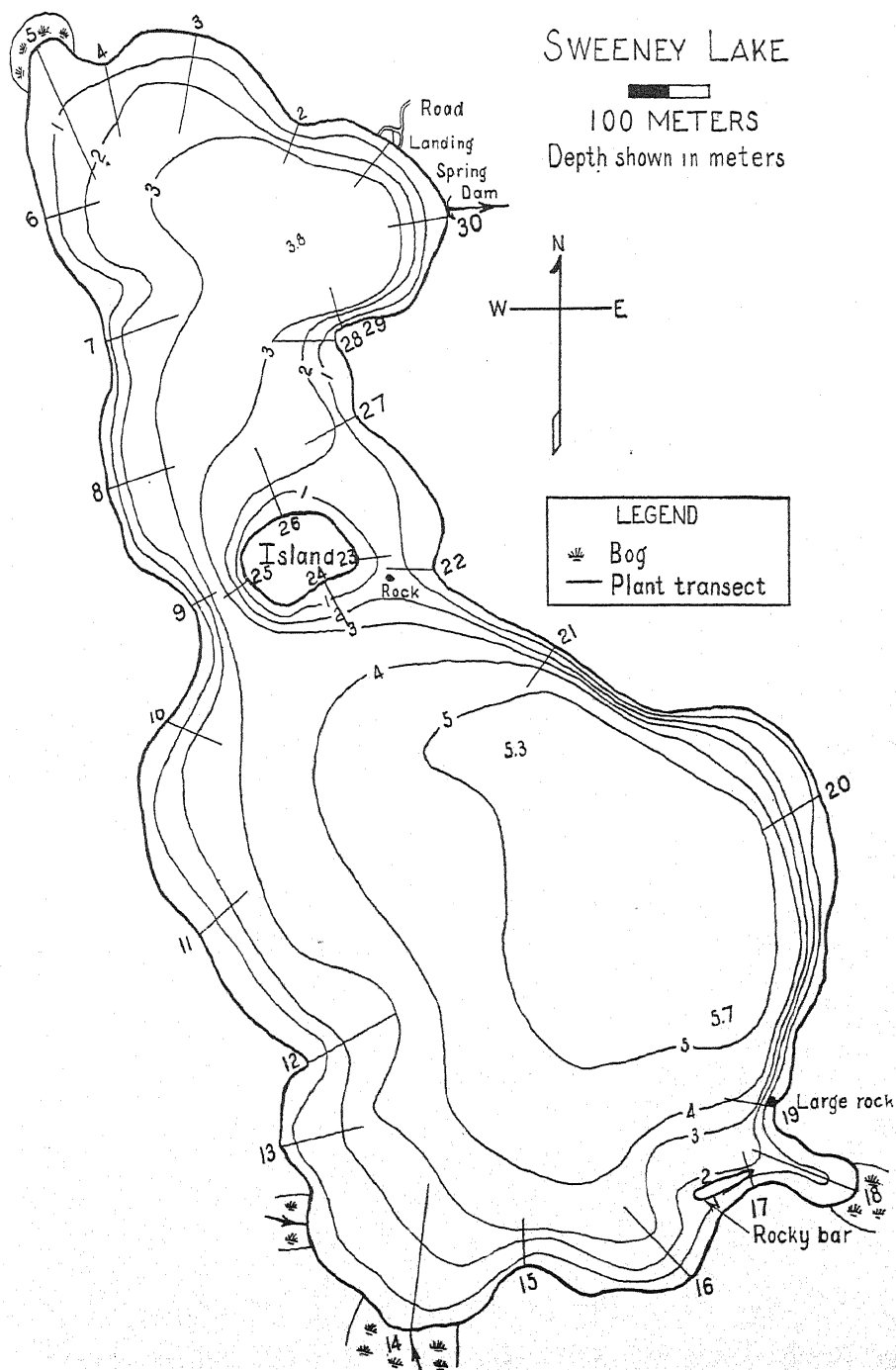
#### THE FLORA AND ITS DISTRIBUTION

In Sweeney Lake twenty-seven species of larger aquatic plants were observed (table 1). In addition, several other species were found growing at the water's edge or only slightly within the water. These have not been listed because they are littoral, swamp or bog plants that were not found in any of the quadrates that were studied.

The methods used in the determination of aquatic plant abundance and its distribution have been discussed in an earlier paper (Wilson, *Ecol. Mono.* 5: 207-247. 1935) and need only to be outlined here. When the lake was first visited it was divided into ecological divisions. Then transects were made through the center of each division and all of the plants

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Fig. 1. Map of Sweeney Lake.





from quadrates of 625 square centimeters in area were collected. The quadrates were placed at intervals as the water deepened by one-fourth meter. The plants from the quadrates were secured by means of a dredge which not only denuded a definite area of the lake floor, but secured a soil sample

TABLE 1  
*Specific crops and their vertical distribution in Sweeney Lake*

SPECIES	SPECIFIC CROP (KILOGRAMS)	PER CENT OF CROP	
		ZONE I (0 TO 1 METER)	ZONE II (1 TO 3 METERS)
<i>Anacharis canadensis</i>	5.320	46	54
<i>Carex</i> sp.	3.294	100	0
<i>Castalia odorata</i>	3.980	28	72
<i>Ceratophyllum demersum</i>	116.267	80	20
<i>Chara</i> sp.	.761	83	17
<i>Dulichium arundinaceum</i>	9.454	100	0
<i>Eleocharis acicularis</i>	.006	100	0
<i>E. palustris</i>	.136	100	0
<i>Equisetum limosum</i>	.532	100	0
<i>Isoetes macrospora</i>	trace	100	0
<i>Myriophyllum spicatum</i>	.931	94	6
<i>Najas flexilis</i>	10.882	87	13
<i>Nymphaeanthus microphyllus</i>	2.729	31	69
<i>N. variegatus</i>	53.889	33	67
<i>Pontederia cordata</i>	13.411	100	0
<i>Potamogeton amplifolius</i>	7.767	58	42
<i>P. gramineus</i> , var. <i>graminifolius</i>	.121	100	0
<i>P. pusillus</i>	33.658	23	77
<i>P. Richardsonii</i>	27.974	47	53
<i>P. Robbinsii</i>	2.261	38	62
<i>P. zosterifolius</i>	1.827	11	89
<i>P. sp.</i>	2.589	88	12
<i>Ranunculus aquatilis</i> , var. <i>capillaceus</i>	.547	100	0
<i>Sagittaria graminea</i>	.609	99	1
<i>Scirpus acutus</i>	20.637	100	0
<i>Typha latifolia</i>	4.287	100	0
<i>Vallisneria</i>	7.894	94	6
TOTAL CROP	331.763	76	24

at the same time. The soil samples were studied in the field and their distribution recorded for correlation with the plants. Each plant collection was washed free from debris in a screen especially constructed to hang over the end of the boat, and then packeted and labeled. At the laboratory the plants in each collection were divided into species and packeted separately. These were dried in the sun and then weighed and recorded.

The estimation of crop abundance was made by totaling the weight of the collections of each species and dividing this weight by the total area

in meters from which it was collected. The estimated total crop in the lake for each species was then found by multiplying the average collection weight per square meter by the total area colonized. This area is determined from hydrographic measurements.

Summary of plant distribution in Sweeney Lake

ZONE I gravel, sand and silt	ZONE II sand, silt	ZONE III organic soil (well decomposed) no plants
<i>Anacharis</i>	<i>Anacharis</i>	
<i>Carex</i> sp.	<i>Chara</i>	
<i>Ceratophyllum</i>	<i>Najas</i>	
<i>Chara</i>	<i>Potamogeton gramineus</i>	
<i>Dulichium</i>	var. <i>graminifolius</i>	
<i>Eleocharis acicularis</i>	<i>P. Richardsonii</i>	
<i>E. palustris</i>	<i>Sagittaria graminea</i>	
<i>Equisetum</i>	<i>Vallisneria</i>	
<i>Isoetes</i>		
<i>Najas</i>		
<i>Pontederia</i>		
<i>Potamogeton amplifolius</i>		
<i>P. gramineus</i>	organic soil	
var. <i>graminifolius</i>	(well decomposed)	
<i>P. pusillus</i>		
<i>P. Richardsonii</i>	<i>Anacharis</i>	
<i>P. Robbinsii</i>	<i>Castalia</i>	
<i>P. zosterifolius</i>	<i>Ceratophyllum</i>	
<i>Ranunculus aquatilis</i> ,	<i>Myriophyllum</i>	
var. <i>capillaceus</i>	<i>Najas</i>	
<i>Sagittaria graminea</i>	<i>Nymphosanthus microphyllus</i>	
<i>S. latifolia</i>	<i>N. variegatus</i>	
<i>Scirpus</i>	<i>Potamogeton amplifolius</i>	
<i>Typha</i>	<i>P. pusillus</i>	
<i>Vallisneria</i>	<i>P. Richardsonii</i>	
	<i>P. Robbinsii</i>	
organic soil	<i>P. zosterifolius</i>	
(well decomposed)		
<i>Anacharis</i>		
<i>Carex</i> sp.		
<i>Castalia</i>		
<i>Ceratophyllum</i>		
<i>Chara</i>		
<i>Dulichium</i>		
<i>Myriophyllum</i>		
<i>Najas</i>		
<i>Nymphosanthus microphyllus</i>		
<i>N. variegatus</i>		
<i>Potamogeton amplifolius</i>		
<i>P. pusillus</i>		
<i>P. Richardsonii</i>		
<i>P. Robbinsii</i>		
<i>P. zosterifolius</i>		
<i>Pontederia</i>		
<i>Ranunculus</i>		
<i>Sagittaria graminea</i>		
<i>Scirpus</i>		
<i>Typha</i>		
<i>Vallisneria</i>		
organic soil		
(not well decomposed)		
<i>Anacharis</i>		
<i>Castalia</i>		
<i>Nymphosanthus microphyllus</i>		
<i>N. variegatus</i>		
swamp and bog		

All of the fixed vegetation of Sweeney Lake is restricted to a zone not exceeding 2.25 meters in depth. This zone skirts the shoreline and the island, and is approximately 190,916 square meters in area. In order that a vertical comparison of the flora could be made the lake profile was

divided into three zones. These zones consist of Zone I (0 to 1 meter), Zone II (1 to 3 meters) and Zone III (3 to 5.7 meters). This division is purely arbitrary, but its comparative value is evident. No fixed vegetation was found in Zone III, but in Zones I and II there is an abundance. In Zone I, 76 per cent of the total estimated crop is concentrated, and in Zone II the remaining 24 per cent is found. The specific crops are shown in table 1. The average yield of dry plant tissue per square meter of the plant zone is 1.73 grams, and the total estimated crop is 331.763 kilograms. This is a comparatively heavy yield for the lakes of the region.

The ecological conditions in the southern portion of the lake, particularly along the south and eastern shores resemble most nearly those of the youthful lakes in the region and the vegetation along these shores is not as dense as in the sheltered areas. With the exception of *Typha* and *Carex*, the species represented here are those listed in the diagram of plant distribution as occurring on gravel, sand and silt. The exposure to wave action is the chief factor in the perpetuation of the inorganic sediments upon which these plants are growing.

In the bays at Stations 5 and 30, and to some extent at Station 18 the soils are of the well decomposed organic type. At these stations those plants listed in the summary of plant distribution as growing on the above soils are very abundant in Zone I and also in Zone II. Near the shoreline at Station 18 where the soils are somewhat more fibrous and at Station 14 the vegetation is practically restricted to the four species listed in the summary of plant distribution as occurring upon only partially decomposed organic soil.

At Stations 27 and 28 large floating mats of *Ceratophyllum demersum* dominated the vegetation. This also extended into Station 26 on the north side of the island. Along the shoreline at this station a wide belt of *Carex* sp. excluded other species of aquatics. It extended into nearly a meter of water as a very dense growth. No fruiting specimens were found to enable identification of the species.

The soils upon which the plants grow in Sweeney Lake may be classed as either mineral or organic in composition. The inorganic soils consist of gravel, sand and silt. Almost no plants were found growing on pure gravel, and those which appeared to be, had their roots anchored in sand and silt. Therefore a two-parted division of the soils may be made for the description of the plant crops occurring in the lake. A comparison of the vegetation growing upon these two soil types was made and in Sweeney

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Fig. 2. A comparison of the per cent of specific crops growing upon various soils in Sweeney Lake.



Lake twenty-two per cent of the total estimated crop was found growing upon sand and silt while the remaining eighty-eight per cent occurred upon organic soils. The specific distribution of plants in the lake is shown in figure 2.

#### COMPARATIVE STUDIES WITH OTHER LAKES OF THE REGION

A lake that has been similarly studied in northern Wisconsin which most nearly resembles Sweeney Lake is Little John Lake in Vilas County (Wilson, l.c.). This lake has a similar geological history and is nearly the same size and depth. In addition it has reached approximately the same stage of sedimentation, and the soils in the shallow water and bays are predominantly of the same finely decomposed organic type. The inlets, however, are not as large and the outlet level has been lowered in recent years by the opening of a beaver dam, which was built across it. The water level of Little John Lake fluctuates considerably with the amount of yearly precipitation. This fluctuation of water level increases the area of wave work upon the shores and only the coarser inorganic soils remain fixed. The organic soils undergo periods of accumulation in the shallow water during years of high water and periods of transportation to lower resting places during the years of low water. This process is most apparent in the open lake and least apparent in the bays.

The effect of the periodic deposition and transportation of organic soils is very marked upon those plants which inhabit sandy soils, for during the periods of deposition they show great decrease in abundance and when the organic soils are swept from the sand they return very rapidly. This change was very marked during the summers of 1933 and 1935.

Like Sweeney Lake, Little John Lake is very turbid during most of its open season and this is due largely to immense quantities of phytoplankton.

The vertical distribution of the vegetation is slightly greater in Little John Lake, but does not extend below three meters. The flora is composed of only thirteen species in contrast to twenty-seven species in Sweeney Lake, and the crop in the latter lake is approximately three times that of the former.

A comparison of the most important crop-producing species in both lakes shows that there is a general agreement in these when they are present in both lakes. In Sweeney Lake, *Ceratophyllum demersum*, *Nymphozanthus variegatus*, and *Potamogeton pusillus* are the three most abundant species while in Little John Lake *Najas flexilis*, *Potamogeton Richardsonii*, and *Nymphozanthus variegatus* are important in the order named. The

above species thrive in the same ecological conditions and indicate the similarity of the two lakes.

Another lake in the region that has been quantitatively studied is Muskellunge Lake in southern Vilas County (Wilson l.c.). This lake presents a marked contrast to Sweeney Lake because of its greater size, depth, transparency of water, and abundance of mineral soils. With the exception of the southern portion, the lake is much younger in the sense of geological maturity. The soils are sandy or stony to a depth of five or six meters, and the least abundant plant species in Sweeney Lake are the important members of the largest portion of Muskellunge Lake. In the shallow bay at the southern end of this lake the soils are largely organic, and slightly resemble conditions in Sweeney Lake. The fluctuating water level, however, brings into action the same factors present in Little John Lake though to an even greater degree. During the summers of 1934 and 1935 wide areas of *Potamogeton Richardsonii*, *P. amplifolius*, *P. Robbinsii*, and *Myriophyllum alterniflorum* were buried beneath a thick mantle of organic sediment that was swept from the shallower water and deposited over the weed beds. At the same time this redistribution of organic soils brought the characteristic flora of the sand areas into prominence.

The aquatic plant community is largely the result of specific sedimentation coupled with certain chemical and physical factors which develop with the maturing of lakes. Comparative geologic maturity of lakes may be suggested by the aquatic flora, but a fuller discussion must be based upon more data than is now available.

#### SUMMARY

1. Sweeney Lake is a typical regional example of a medium hard water lake of the drainage type in a mature stage of development.

2. The larger aquatic vegetation of this lake is abundant and is composed of twenty-seven species, which occupy the lake soils to a depth of two and one-fourth meters. The total dry weight of the crop is estimated to be 331.763 kilograms and the average dry weight per square meter of the colonized area is estimated to be 1.73 grams.

3. The most abundant plant species are those which attain greatest development upon well decomposed organic soils, while the least abundant are those characteristic of aquatic sand areas. It is suggested that the former represents the characteristic vegetation of a lake in an advanced stage of development and the latter the common vegetation of the primitive or youthful lake.

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The writer wishes to express his appreciation to the Wisconsin Geological and Natural History Survey for the opportunity and facilities for studying the problems of lake ecology in the Highland Lake District of Wisconsin, and particularly to Dr. E. A. Birge and to Prof. Chancey Juday for valuable advice and discussion during the direction of the work.

COE COLLEGE,

CEDAR RAPIDS, IOWA

# Inheritance of resistance to the loose and covered kernel smuts of sorghum

## I. Dwarf Yellow Milo hybrids<sup>1</sup>

D. ELIZABETH MARCY

(WITH PLATES 5 AND 6, AND TWO TEXT-FIGURES)

Disease resistance presents a particularly interesting type of genetic problem, since it concerns two diverse organisms, host and parasite, each with its own genotype, and each affected differently by environal influences. Two early workers demonstrated both the simplicity and the complexity which may be encountered in a genetic study of resistance Biffen (1905, 1907, 1912) discovered that the finely adjusted relationship between the host (wheat) and an obligate parasite (yellow rust) might be governed by a single Mendelian factor, while Nilsson-Ehle (1911), from his study of the reaction of wheat hybrids to stripe rust, concluded that multiple factors must be involved. These initial experiments have stimulated studies on the inheritance of resistance to many plant diseases. By far the most detailed and complete have been made on the inheritance of resistance to the rusts and smuts in the cereal grains. Since the present investigation deals with the inheritance of resistance to smut in sorghum, a brief reference to similar studies with the smuts of cereals will be made.

Extensive data on the inheritance of resistance to bunt of wheat, *Tilletia Tritici* and *Tilletia laevis*, have been procured. Gaines (1918, 1920, 1923, 1925<sup>a</sup>, 1925<sup>b</sup>) and others have obtained a wide range of infection percentages and have concluded that bunt reaction was governed by several factors. Others have procured simple clear cut ratios and Briggs (1926, 1930<sup>a,b,c</sup>, 1931, 1932<sup>a,b</sup>, 1933, 1934) has succeeded in identifying three distinct factors for resistance. There is some evidence that resistance to several races of the two smuts may be governed by the same factor (Smith, 1933). Wismer (1934) has reported that there is no correlation between reaction to bunt and reaction to leaf rust, and Hayes, Ausemus, Stakman and Bamberg (1934) found that reaction to bunt was independent of the reaction to stem rust, leaf rust, and black chaff in their crosses. The influence of environment upon the expression of factors for resistance in certain crosses has been ascertained by experiments in Fall and Spring sowing (Gaines, 1923, 1925<sup>b</sup>, and Gaines and Singleton, 1926).

Resistance of oat hybrids to the loose and covered smuts, *Ustilago Avenae* and *Ustilago levis* has been the subject of thorough research particularly by Reed (1925, 1928, 1931, 1932<sup>a,b</sup>, 1934, 1935). He has shown that in many crosses, principally those involving Black Mesdag as the

<sup>1</sup> Brooklyn Botanic Garden Contributions No. 75.



resistant parent (Reed, 1925, 1928, 1934), resistance was dependent upon a single dominant factor. Von Rosenstiel (1929) also found this to be true for Black Mesdag hybrids. Many other workers have concluded that resistance to one or the other smut was governed by two or more factors, and some have presented evidence that modifying factors are present. A series of crosses have been made by various workers using Markton as the resistant parent. Many of these data have not been interpreted. Coffman, Stanton, Bayles, Wiebe, Smith and Tapke (1931) postulated a two factor hypothesis for crosses with Scottish Chief. Stanton, Reed and Coffman (1934) suggested that Markton and Black Mesdag contain complementary factors for resistance. Schattenberg (1934) believed that Markton had three factors for resistance.

In most cases the reaction of hybrid plants to one smut has been found to be entirely independent of their reaction to the other (Reed, 1931, 1932<sup>b</sup>; Stanton, Coffman and Tapke, 1934; Stanton, Reed and Coffman, 1934), but for Black Mesdag hybrids it has been found to be correlated (Reed, 1928, 1934; Welsh, 1931).

The most important genetic studies on the resistance of maize to corn smut, *Ustilago Zeae*, were made by Immer (1927) and Hoover (1932). Immer established linkage relations between susceptibility and the morphological characters, liguleless, brachytic and red pericarp. Hoover tested the relation of susceptibility to nine of the maize linkage groups. Linkage was definitely established with groups IV (liguleless) and VI (brachytic) in agreement with Immer's work, and with groups VII (ramosa) and IX (tassel seed), all linkage groups which possess morphological characters favoring infection. He was led to believe that reaction to smut depends upon two sets of factors, one set controlling the physiological and the other the morphological characters of the plant.

Because of the difficult methods of inoculation, very limited genetic studies have been undertaken on the resistance of wheat to the loose smut, *Ustilago Tritici*, and of barley to the covered smut, *Ustilago Hordei*, but the heritable nature of smut resistance has been demonstrated.

#### RESISTANCE OF SORGHUM HYBRIDS TO THE COVERED SMUT

Very few investigators have studied the inheritance of resistance of sorghums to smut diseases. Using covered smut, Reed (1929, 1930) observed that infections were high in the  $F_2$  generation of crosses between the resistant Feterita and susceptible varieties as compared with that of crosses between Milo and susceptible varieties. In the  $F_2$  generation, Feterita hybrids frequently gave more than 50 per cent infection, Milo hybrids always less than 25 per cent. He concluded that susceptibility was domi-

nant in the Feterita hybrids and recessive in the Milo hybrids and that were it possible to infect the susceptible parents 100 per cent, 75 per cent infection might have been obtained for the former hybrids, 25 per cent for the latter.

Swanson and Parker (1931) inoculated  $F_3$  progenies of a cross between Red Amber Sorgo, susceptible, and Feterita, resistant, with the covered smut and found that approximately three-fourths of the progenies contained smutted plants although none were more than 10 per cent infected.

There have been no reports on the inheritance of resistance to the loose smut except brief résumés made by the writer from time to time (Plant Pathology, Brooklyn Botanic Garden Record, 1932-1936).

#### MATERIAL AND METHODS

*Types of crosses.* The present investigation deals with the reaction of sorghum hybrids to the covered and loose kernel smuts. The true breeding varieties of sorghum (*Andropogon Sorghum* (L.) Brot.) used in these crosses were supplied by Dr. George M. Reed at the Brooklyn Botanic Garden where these investigations were undertaken.

Sorghum is normally self pollinated, but as much as five per cent field cross pollination may occur (Sieglinger, 1921). To prevent this, heads to be used for seed were bagged as soon as they began to flower. Hybrids were obtained according to the method outlined by Reed (1930), by which seedling color is used as a hybrid detector.

On account of the difficulty in securing them, only a small number of  $F_1$  plants were inoculated, but these were grown in 1934 and 1935 when experimental conditions were very favorable for infection. The reaction of  $F_2$ ,  $F_3$  and, for some hybrids,  $F_4$  and  $F_5$  generation plants was determined. The hybrids studied may be divided into three main categories as follows:

- A. Crosses between resistant varieties  
Feterita  $\times$  Dwarf Yellow Milo and reciprocal
- B. Crosses between Dwarf Yellow Milo and susceptible varieties  
\*Dakota Amber Sorgo  $\times$  Dwarf Yellow Milo  
Shallu  $\times$  Dwarf Yellow Milo and reciprocal  
\*Dawn Kafir  $\times$  Dwarf Yellow Milo and reciprocal
- C. Crosses between Feterita and susceptible varieties  
\*Feterita 182  $\times$  Sumac Sorgo  
Dakota Amber Sorgo  $\times$  Feterita 182  
Shallu  $\times$  Feterita 182  
\*Dawn Kafir  $\times$  Feterita 12 and \*reciprocal

\* Crosses made by Dr. George M. Reed and  $F_1$  heads available in his laboratory.

In all but one case the same susceptible variety has been crossed with each resistant type. Crosses in the first two categories will be considered in the first part of this report.

*Sorghum smuts.* The two smuts of sorghum, *Sphacelotheca Sorghi* (Link) Clinton (the covered kernel smut) and *Sph. cruenta* (Kühn) Potter (the loose smut), have been known in America for many years, the covered smut being the more widespread and destructive. Chlamydospores of these smuts were procured from Dr. Reed. They have been used by him for more than fifteen years. In recent years physiologic races of both smuts have been discovered, but the spore material provided for these studies comprised only the common, most widely distributed race of *Sph. Sorghi*, form 1, and a race of *Sph. cruenta* to which Feterita is resistant. A fresh supply was procured each year from the susceptible varieties Dawn Kafir and Dakota Amber Sorgo.

*Procedure.* The method of inoculation was uniform throughout. Seeds were dusted with dry spores obtained by grinding smutted panicles of the previous season in a mortar and sifting out the debris. Care was taken not to mix the two smuts. No spore material was used if samples failed to show good germination in distilled water.

The seeds were germinated in builders' sand which would pass through a 20 but not a 40 mesh sieve. It was washed, thoroughly air dried, and water or sucrose solutions, as indicated later, were added in definite percentages of the total water holding capacity. The sand was thoroughly mixed to assure an even moisture, and the inoculated seed planted one inch deep in paraffined paper cups. The cups were placed in moist chambers and the latter partially immersed in tanks of water kept at a constant temperature (Faris, 1924). Thus a perfect water seal was formed, and almost no evaporation took place. When the seedlings emerged, they were watered and placed in the greenhouse until large enough to be transplanted to the field. Moisture and temperature were, therefore, carefully controlled until the young shoots reached the length of one inch, but not in any way thereafter.

Striking differences in the percentages of infection of susceptible varieties may be brought about by changes in the environment during the germination period. Reed and Faris (1924) found that a slightly acid soil reaction and low moisture was most favorable for infection and that, within the temperature range for spore germination, the optimum temperature for infection depended upon the host variety. With changes in the seedling environment, susceptible varieties gave infections ranging from 0 to 93.8 per cent, but resistant varieties maintained their resistance. Conditions favorable for infection with *Sph. Sorghi* were also favorable

for infection with *Sph. cruenta*. In the course of the present investigations further experiments have resulted in modifications of this method. Seeds were germinated at 18–23° C. in sand, with 20 per cent moisture in 1931, 30 per cent moisture in 1932, and 10 per cent moisture in 1933, and 10 per cent moisture supplied as a 2 per cent sucrose solution in 1934 and 1935. The reaction of the sand at time of planting was approximately neutral.

Parents and hybrids grown in any one year were all subjected to the same environment. Changes were made from year to year because incidental tests with the parental varieties indicated that these modifications yielded, in general, higher percentages of infection. Consequently, fewer susceptible plants escaped infection during the latter years, and therefore results (particularly for 1934 and 1935) were definitely more accurate, as regards a genetic analysis, than those of the preceding years. The effects of these differences in environment will be more clearly shown in the discussion of results with parental varieties and hybrids.

Each year plants were grown at the Brooklyn Botanic Garden. Additional plants were grown at Ridgewood, N. J., in 1931, and at Farmingdale, Long Island, in 1934 and 1935. A comparison of infection results in the different fields showed no difference.

#### INFECTION RESULTS WITH PARENTAL VARIETIES

*Susceptible varieties.* The four susceptible varieties used (Shallu 196 (C.I. 85)), Dakota Amber Sorgho 48 (Texas A.E.S.), Dawn Kafir 186 (C.I. 340), and Sumac Sorgho 139 (F.C.I. 1831), represented widely different types of sorghum that differ also in their "degree of susceptibility." The actual infection data are given in tables 3 and 4, but are shown diagrammatically in figure 1.

The reaction to the two smuts corresponds closely, a variety giving high infections with one smut tending to give high infections with the other, except that percentages of infection with *Sph. cruenta* were always lower. In general, higher infection percentages were obtained by Reed under controlled germination conditions than under field conditions. The present investigations show that in the *Sph. Sorghi* series infection percentages were nearly always higher when the seeds were germinated in sand with 10 per cent moisture supplied as a sucrose solution than when germinated under any of the other moisture conditions, although in the *Sph. cruenta* series this was not consistently true. Since the temperature and moisture were controlled only during the germination period, it seems reasonable to assume that during this period the external environment has its most important effect upon the amount of smut produced.

As conditions became more favorable for seedling infection, more nearly the same percentages of smutted plants were obtained for all four varieties. This demonstrates that each of these varieties was genetically susceptible, i.e. provided an internal environment favorable for the development of the fungus. The results obtained emphasize the importance of supplying an environment favorable for the full expression of genetic

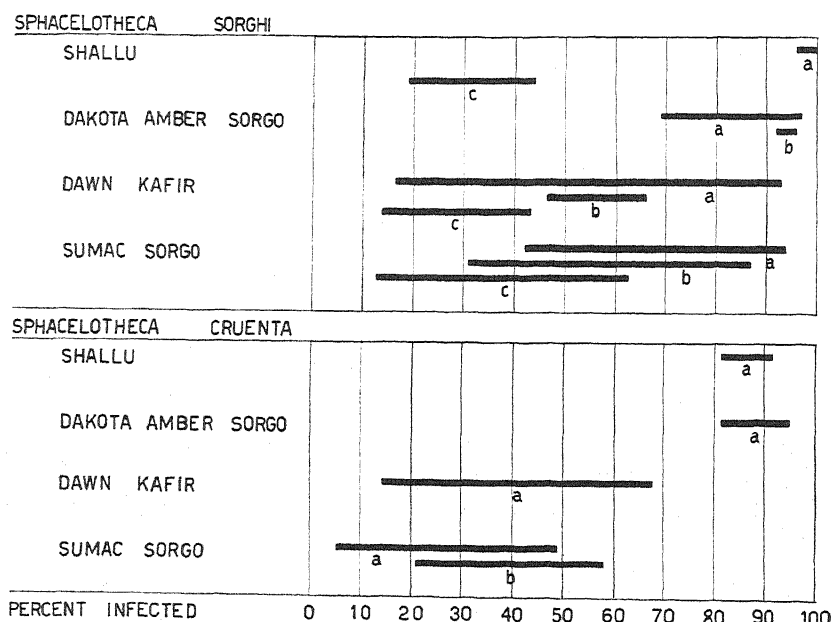


Fig. 1. Range of infection percentages for susceptible sorghum varieties.

a. Controlled germination conditions, 1931-1935.

b. Controlled germination conditions (Reed, 1930, and unpublished data).

c. Field conditions (Reed, 1923; Reed and Melchers, 1925).

factors for susceptibility. The accuracy of results with hybrids depends upon the extent to which the susceptible parent approaches 100 per cent infection when grown under the same enviroinal conditions.

*Resistant varieties.* The resistant varieties used were Dwarf Yellow Milo 124 (C.I. 332), and two strains of Feterita, 182 (C.I. 182) and 12 (Farm Crops Dept., Univ. of Mo.). Reed (1923, 1930), Reed and Faris (1924) and Reed and Melchers (1925) determined their reactions to the two smuts. Seeds were germinated under field conditions and also under controlled temperature and moisture conditions favorable for infection. When inoculated with either smut, all plants of Dwarf Yellow Milo were normal, results similar to those obtained by Kulkarni (1924). In the pres-

ent studies 328 plants of Dwarf Yellow Milo inoculated with *Sph. Sorghi* failed to produce any smut, but one smutted plant occurred out of 242 inoculated with *Sph. cruenta*. This appeared when germination conditions were most favorable for infection.

The resistance of Feterita was not quite so complete. Reed *et al.* found that Feterita 182 was free of smut except under conditions very favorable for infection, when occasional plants were smutted with *Sph. Sorghi*. The same was true of Feterita 12. Some of these infected plants had a few normal seeds and were proved to be true Feterita. Results therefore indicated that neither strain of Feterita was entirely resistant to *Sph. Sorghi* when germinated under conditions favorable for infection. When these two strains of Feterita were inoculated with *Sph. cruenta* no plants of strain 182, but a few of strain 12, were infected. Kulkarni (1924) noted that occasional plants of Feterita might be infected with either smut.

Further results have been obtained in these investigations. In 1931 and 1932, 247 inoculated plants were grown and one was infected. In 1933, when the moisture supplied during germination was reduced to 10 per cent, the influence of environment was found to be more striking. In 1933, no plants were smutted out of the 80 grown, but certain of the plants inoculated with *Sph. Sorghi* produced partially or completely blasted heads, although no actual counts were taken. In 1934, out of 291 plants, 39.1 per cent were blasted, and in 1935, out of 59 plants, 44.1 per cent. The number of typically smutted plants did not increase, 1.7 per cent occurring in 1934 and none in 1935. The occurrence of smut balls in some of the blasted heads demonstrated that blasting was a pathological condition due to infection. Plants exhibiting this effect were also characterized by excessive tillering, and branching from the upper nodes, after the main head had failed to develop properly. Normal and blasted plants were of about the same height. Smut balls were often present on tiller heads though the main head lacked them, but tillers might also produce more normal seed than the main head. A typically blasted plant, in contrast to one left uninoculated, is shown in plate 5. An enlarged view of the main head and two of the tillers (plate 6) shows the blackened ends of the blasted spikelets in the main head, and in the tillers the presence of normal, blasted, and smutted spikelets. Plants were classified as "blasted" if any noticeable number of the flowers on any head had failed to develop, even though smut balls might also be present. They were classified as smutted only when they produced typically smutted heads.

Results therefore indicated that when germinated under environmental conditions favorable for heavy infection of susceptible varieties, Feterita might also become infected with *Sph. Sorghi*. On the other hand, the

peculiar type of infection demonstrated that they provide an unfavorable internal environment for the full development of the parasite once it has entered, and therefore possess a protoplasmic resistance. In respect to resistance to this smut, Feterita must therefore differ genetically from Milo which, under like conditions, has consistently failed to show any such symptoms of disease, and also from truly susceptible varieties which allow for normal fruition of the fungus. There is no reason to think that the infection of Feterita reported here is due to the presence of a different race of smut, for Feterita is not infected except when a particular, rather specialized, environment is provided.

No such symptoms of infection occurred when Feterita was inoculated with *Sph. cruenta*. In the present investigations a total of 500 plants of strain 182 were grown and none were smutted. Strain 12, however, was not entirely free of smut. Twenty-one plants were grown in 1931 and 4.7 per cent were infected, 18 in 1932 and none were infected, and 35 in 1935 and 17.1 per cent were infected. There may, therefore, be a genetic difference between these strains of Feterita in respect to reaction to *Sph. cruenta*. No blasting appeared among any of the plants inoculated with *Sph. cruenta*.

#### INFECTION RESULTS WITH HYBRIDS BETWEEN RESISTANT VARIETIES

*Feterita* × *Dwarf Yellow Milo* and *reciprocal*. Infection results with the resistant varieties Dwarf Yellow Milo and Feterita have led to the supposition that they may possess different factors for resistance. Consequently, reciprocal crosses have been made between them.

#### *Reaction to Sphacelotheca Sorghi*

*F<sub>1</sub> generation.* No inoculated *F<sub>1</sub>* plants have been grown.

*F<sub>2</sub> generation.* In 1932 and 1933, 174 *F<sub>2</sub>* plants of *Feterita* × *Dwarf Yellow Milo* and 170 of the reciprocal hybrid were grown. None were infected, nor did either parent produce any smutted plants. In 1934 and 1935 (table 1), when environal conditions were more favorable for infection, approximately 1/16th of the hybrid plants were typically smutted. This was considerably larger than the proportion of infected Feterita plants, suggesting the segregation of duplicate factors for resistance. The number of blasted plants among the hybrids was extremely small, indicating that the factor for resistance from Dwarf Yellow Milo is epistatic to the factor

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#### Explanation of plate 5

- A. Feterita plant inoculated with *Sph. Sorghi* showing blasted heads.
- B. Feterita plant uninoculated.



MARCY: RESISTANCE TO SMUTS



for resistance from Feterita. It is possible that if Feterita was giving 100 per cent blasted heads, the number of blasted  $F_2$  plants might approximate  $3/16$ ths.

*F<sub>3</sub> generation.* Two sets of inoculated  $F_3$  progenies were grown, the first set in 1933 when enviroinal conditions were such that no blasted heads appeared, the second set in 1934 when conditions were favorable for the production of blasted and typically smutted heads. Both sets were from the 1932 and 1933 series of  $F_2$  plants which had failed to produce any infected individuals. Twenty seeds of each progeny were planted and in almost every case 15 to 20 plants reached maturity.

TABLE 1

*Infection results with Sphacelotheca Sorghi for the hybrid Feterita × Dwarf Yellow Milo and its reciprocal. F<sub>2</sub> generation—1934, 1935*

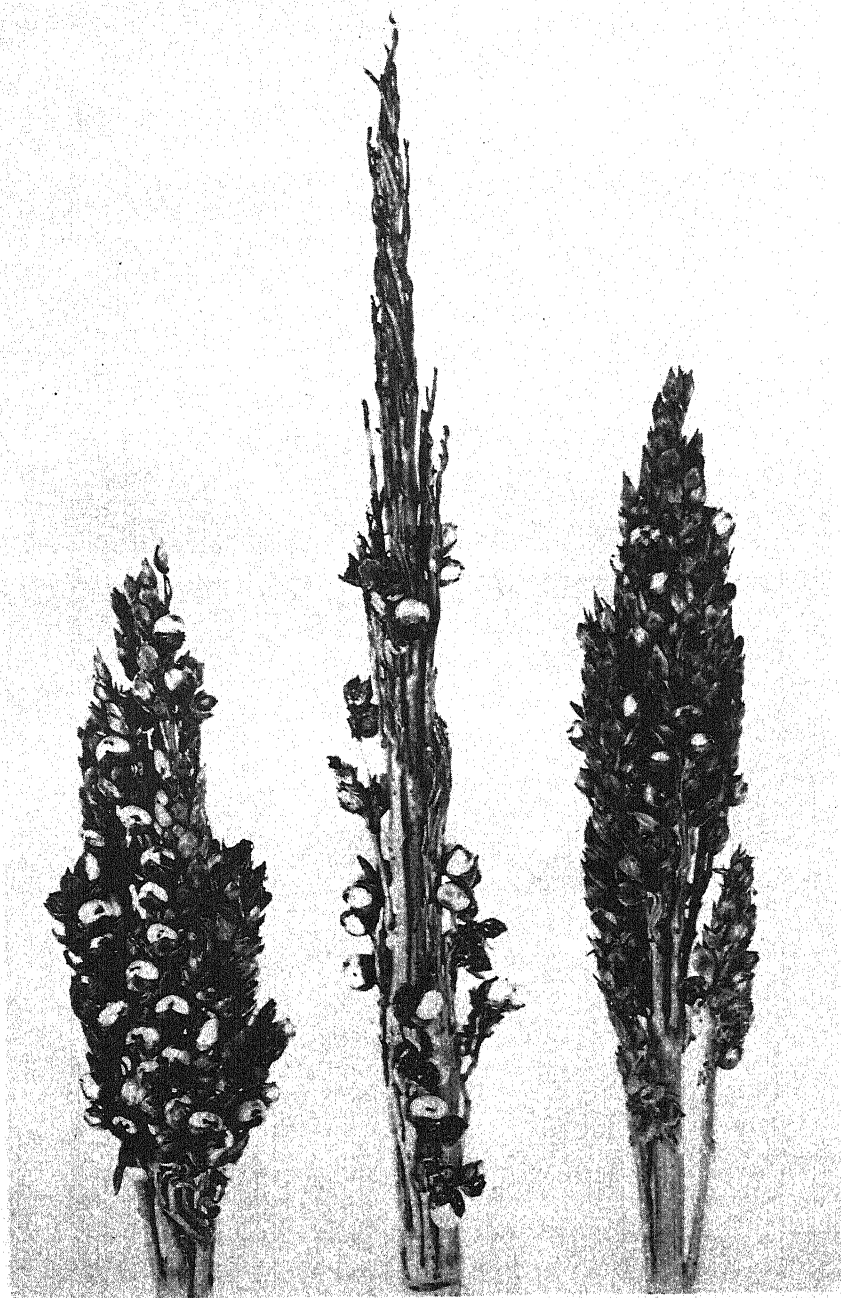
	NO. PLANTS	NO. NORMAL	NO. BLASTED	NO. TYPICALLY SMUTTED	PER CENT TYPICALLY SMUTTED
Hybrids					
Feterita 182 × Dwarf Yellow Milo	71	66	2	3	4.2
Dwarf Yellow Milo × Feterita 182	68	63	2	3	4.4
Two hybrids combined	139	129	4	6	4.3
Calculated 12:3:1 ratio	139	104.4	26.1	8.7	
Parents					
Feterita 182	350	205	140	5	1.4
Dwarf Yellow Milo	253	253	0	0	0

*Results with the 1933 set.* There were 56 progenies in all, 28 of each hybrid. Five of the first 28 progenies produced smutted plants, giving 5.5, 5.8, 7.1, 17.6, and 31.2 per cent infection respectively. One of the other 28 progenies gave 10.5 per cent smutted plants, the rest of the progenies remaining free from smut. Of the 56 progenies, therefore, 6 failed to breed true for resistance.

*Results with the 1934 set.* There were 35 progenies, 17 of Feterita × Dwarf Yellow Milo and 18 of the reciprocal hybrid. The results are recorded in table 2. Seven progenies out of the 35 produced smutted plants, a much larger proportion than in 1933. It is interesting to compare the actual results with the expected distribution of  $F_3$  progenies on the basis of the two-factor hypothesis suggested, R representing the milo factor and B the Feterita factor.

#### Explanation of plate 6

Enlarged view of the main head and two tillers of the plant represented in Plate 5, A.



MARCY: RESISTANCE TO SMUTS

TABLE 2

*Infection results with Sphacelotheca Sorghi for the hybrid Feterita×Dwarf Yellow Milo and its reciprocal. F<sub>3</sub> generation progenies—1934*

Six progenies of this hybrid and 3 of the reciprocal cross produced no plants that were smutted, but small numbers that were blasted; 7 progenies of the hybrid and 12 of the reciprocal contained neither smutted nor blasted plants. Infection reactions for the other progenies are as follows:

PROGENT NO.	NO. PLANTS	NO. BLASTED	NO. TYPICALLY SMUTTED	PER CENT TYPICALLY SMUTTED
Feterita×Dwarf Yellow Milo				
32-23	11	1	1	9.0
32-46	13	9	1	7.6
32-61	14	2	2	14.2
33-3	11	0	1	9.0
Dwarf Yellow Milo×Feterita				
32-2	14	1	2	14.2
32-40	17	8	2	11.7
32-65	12	1	1	8.3

F<sub>2</sub> genotypes

1 RRBB

2 RRbB

2 RrBB

4 RrBb

1 RRbb

2 Rrbb

1 rrBB

2 rrBb

1 rrbb

Segregation of F<sub>3</sub> progenies

All resistant

All resistant

3:1 resistant to blasted

12:3:1 resistant, blasted, smutted

All resistant

3:1 resistant to smutted

All blasted

3:1 blasted to smutted

All smutted

Since blasting occurs in only about 50 per cent of the plants possessing the B factor, it is impossible to accurately classify the progenies as to segregation for blasting. It is probable that many progenies which were entirely normal should have contained some blasted plants. For this reason, no distinction will be made between normal and blasted plants and only the relation of normal to typically smutted plants will be considered. In regard to typical smut infection, F<sub>2</sub> plants gave rise to two types of F<sub>3</sub> progenies, those which bred true for resistance and those which produced small numbers of smutted individuals. No progenies were more than 50 per cent infected, so it is obvious that no fully susceptible F<sub>3</sub> progenies of the genotype, rrbb, were represented in this sample. Four-sixteenths of the progenies should have given 6.25 per cent infection. There were so few plants per progeny that the chances of this small percentage of smutted plants appearing was slight. Four-sixteenths, or 9 progenies of the 1934 series

should have given 25 per cent smutted plants. Smut was actually present in 7 progenies. From 1934 data, therefore, the number of progenies containing smutted plants closely approximates the number expected to give 25 per cent infection. If 1933 data are considered, the number of progenies containing smutted plants was considerably less, and closely approximates the number expected to give 25 per cent infection, if there was segregation of three factors for resistance. Because the enviroinal conditions supplied in 1934 were more favorable for infection, 1934 data have been considered the more reliable.

*F<sub>4</sub> generation.* Representatives of certain of these F<sub>3</sub>'s were tested in the F<sub>4</sub> generation. An F<sub>4</sub> family was grown from each of 27 survivors of 4 F<sub>3</sub> progenies which had given from 5.5–17.6 per cent infection. These produced two types of F<sub>4</sub> families, smut-free and containing smutted plants, blasted heads being present in both groups. An F<sub>4</sub> family was also grown from each of 33 survivors of 7 F<sub>3</sub> progenies which had been free of smut. These bred true for resistance in the F<sub>4</sub> generation, but a few of them contained blasted plants.

Results with these crosses have therefore provided genetic evidence that the two resistant varieties, Feterita and Dwarf Yellow Milo, possess different factors for resistance. Further, it has been demonstrated that the Milo factor is epistatic to the Feterita factor.

#### *Reaction to Sphacelotheca cruenta*

*F<sub>1</sub> generation.* The one inoculated F<sub>1</sub> plant proved to be normal.

*F<sub>2</sub> generation.* In 1932, 99 plants of Feterita × Dwarf Yellow Milo and 101 of the reciprocal hybrid were inoculated with *Sph. cruenta*. None of these plants were infected. In 1935, 48 plants of the hybrid and 53 of its reciprocal were again inoculated, and none were infected. No infected plants were found in any rows of Feterita or of Dwarf Yellow Milo grown during the same years.

*F<sub>3</sub> generation.* In 1935, F<sub>3</sub> results were obtained for 15 F<sub>3</sub> progenies of Feterita × Dwarf Yellow Milo and for 14 of the reciprocal, all descendants of the 1932 *Sph. cruenta* series. In nearly every case each progeny was represented by 15–25 individuals, totaling 418 plants. None were infected. The parents were also free of smut and there was none of the blasting characteristic of Feterita when inoculated with *Sph. Sorghi*, present in any plants of Feterita or any of the F<sub>2</sub> or F<sub>3</sub> hybrids. It may be concluded, then, that Feterita and Dwarf Yellow Milo have in common at least one factor for resistance to *Sph. cruenta* and that a cross between them gives only genetically resistant hybrids.

INFECTION RESULTS WITH HYBRIDS BETWEEN THE RESISTANT VARIETY DWARF YELLOW MILO AND SUSCEPTIBLE VARIETIES

*Reaction to Sphacelotheca Sorghi*

*F<sub>1</sub> generation.* There were 18 *F<sub>1</sub>* plants of crosses between Dwarf Yellow Milo and the susceptible varieties Dakota Amber Sorgo and Dawn Kafir, all of which were normal, suggesting the dominance of resistance.

*F<sub>2</sub> generation.* Infection data for the three crosses between susceptible varieties and Dwarf Yellow Milo, along with the parental varieties, are

TABLE 3

*Infection results with *F<sub>2</sub>* plants and parental varieties of hybrids between Dwarf Yellow Milo and susceptible varieties, inoculated with *Sphacelotheca Sorghi**

HYBRID	YEAR	<i>F<sub>2</sub></i> PLANTS			SUSCEPTIBLE PARENTAL VARIETIES		
		NO. PLANTS	NO. INF.	PER CENT INF.	NO. PLANTS	NO. INF.	PER CENT INF.
Dakota Amber Sorgo × *Dwarf Yellow Milo	1931	73	10	13.7	14	13	92.8
	1932	55	4	7.3	22	20	90.9
	1933	62	7	11.3	29	20	68.9
	1934	43	9	20.9	112	109	97.3
	1935	33	5	13.1	45	37	82.2
	Total	271	35	12.9	222	199	89.7
Shallu × Dwarf Yellow Milo	1934	67	12	17.9	33	33	100.0
	1935	24	4	16.6	30	29	96.6
	Total	91	16	17.6	63	62	98.4
Dwarf Yellow Milo × Shallu	1934	73	16	21.9			
	1935	17	1	5.8			
	Total	90	17	18.9			
Dawn Kafir × Dwarf Yellow Milo	1931	87	3	3.5	42	20	47.6
	1932	97	5	5.2	36	6	16.6
	1933	51	7	13.7	36	24	66.6
	1934	8	2	25.0	142	132	93.0
	1935	12	1	8.3	51	44	86.3
	Total	255	18	7.1	307	226	73.6
Dwarf Yellow Milo × Dawn Kafir	1933	74	6	8.1			
	1934	43	6	14.0			
	1935	25	3	12.0			
	Total	142	15	10.6			

\* 328 plants of Dwarf Yellow Milo were grown, 1931-1935, and none were infected.

given in table 3. Preliminary results with these hybrids have been obtained by Reed (1929, and unpublished data) and are referred to in the present discussion of these hybrids.

The  $F_2$  generation of the cross Dakota Amber Sorgo  $\times$  Dwarf Yellow Milo produced as high as 20.9 per cent smutted plants in the year when the susceptible parent gave 97.3 per cent infection. Reed found that out of a total of 200 plants of this hybrid 17.7 per cent were smutted, the susceptible parent giving 94.7 per cent infected plants, the resistant parent none. When all of the Shallu plants were smutted, 21.9 per cent of the  $F_2$  generation plants of one of the Shallu-Milo hybrids were infected. Approximately 100 inoculated  $F_2$  plants of the hybrid Dawn Kafir  $\times$  Dwarf Yellow Milo were grown by Reed, and 8.5 per cent were diseased, 56.9 per cent of the Dawn Kafir plants being infected and none of Dwarf Yellow Milo. In the present investigations, Dawn Kafir also did not show quite as high infections as the other two susceptible varieties, and the Dawn Kafir-Milo hybrids averaged only 7.1 and 10.6 per cent. But in 1934 when infections with the susceptible parent were highest (93.0 per cent), the hybrid gave 25 per cent. The results indicate, as suggested earlier by Reed (1929, 1930) that there is segregation of a single dominant factor for resistance in these Milo hybrids. A study of  $F_3$  generation data is necessary to verify this.

Investigations in the  $F_3$  and  $F_4$  generations have been carried out for the hybrid Dakota Amber Sorgo  $\times$  Dwarf Yellow Milo and in the  $F_3$  generation for Dawn Kafir  $\times$  Dwarf Yellow Milo. For each progeny 15 to 20 plants reached maturity.

*F<sub>3</sub> generation of Dakota Amber Sorgo  $\times$  Dwarf Yellow Milo.* In 1933, 30  $F_3$  progenies inoculated with *Sph. Sorghi* were grown from survivors of an  $F_2$  generation which had given 7.3 per cent infection with *Sph. Sorghi*. In 1934 progenies of 11 additional survivors were grown, and also progenies from 18 survivors of another set of  $F_2$ 's of the same cross which had given 19.2 per cent infection with *Sph. Sorghi*. The progenies have been grouped in 5 per cent classes on the basis of infection percentages obtained, and the number of progenies in each class is shown in figure 2, A. Results for both years are included. The 6 progenies which had more than 50 per cent infected plants were all survivors of the  $F_2$  series which had given only 7.3 per cent infection, and therefore probably belonged to the homozygous susceptible group, representing  $F_2$  plants which had escaped infection. If progenies which gave from 1-50 per cent infection are considered segregating, the distribution of resistant to segregating progenies is suggestive of a 1:2 ratio, which would be expected if there was segregation of a single dominant factor for resistance in this cross. Of progenies in the 1-50 per

cent group, 568 plants averaged 16.4 per cent infection, very near the average of 17.3 per cent obtained for the  $F_2$ 's grown in 1933 and 1934. Those in the 50-100 per cent group averaged 64.4 per cent infection, while three adjoining rows of the susceptible parent gave from 60.0 to 85.7 per cent infection, averaging 72.7 per cent.

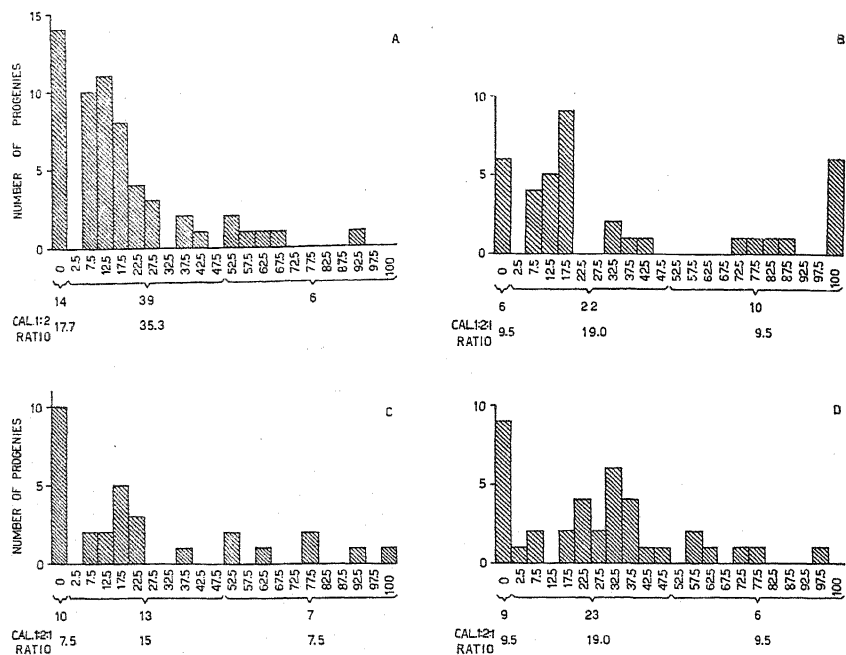


Fig. 2. Distribution of  $F_3$  progenies into 5 per cent infection classes

A. Dakota Amber Sorgo  $\times$  Dwarf Yellow Milo.  $F_3$  progenies inoculated with *Sphacelotheca Sorghi*. Grown from survivors of inoculated  $F_2$  plants.

B. Dakota Amber Sorgo  $\times$  Dwarf Yellow Milo.  $F_3$  progenies inoculated with *Sph. Sorghi*. Grown from uninoculated  $F_2$  plants.

C. Dawn Kafir  $\times$  Dwarf Yellow Milo.  $F_3$  progenies inoculated with *Sph. Sorghi*. Grown from uninoculated  $F_2$  plants.

D. Dakota Amber Sorgo  $\times$  Dwarf Yellow Milo.  $F_3$  progenies inoculated with *Sph. cruenta*. Grown from uninoculated  $F_2$  plants, the same as those represented in B.

$F_3$  progenies were also grown from uninoculated  $F_2$ 's, 20 seeds from each of 38  $F_2$  heads being inoculated with *Sph. Sorghi*, and grown in 1934. The class distribution, on the basis of 5 per cent infection differences is shown in figure 2, B. There is a clear-cut separation between the segregating and susceptible groups, no progenies occurring between 45 and 70 per cent, and

the agreement to a 1:2:1 ratio is reasonably good. The 10 families in the susceptible group gave an average of 91.4 per cent infection while a row of the susceptible parent gave 85.7 per cent infection. Infections in the segregating group ranged from 5 to 45 per cent averaging 18.8 per cent for the 22 segregating families, while  $F_2$ 's grown in the same year gave 20.9 per cent infection. This evidence again indicates segregation of a single factor for resistance.

*F<sub>4</sub> generation of Dakota Amber Sorgo × Dwarf Yellow Milo.* In 1934 representatives of the susceptible and segregating groups were tested for their reaction to *Sph. Sorghi* in the  $F_4$  generation.

I.  $F_4$  families were grown from 4 survivors of one of the  $F_3$  progenies which had given 55 per cent infection. One family was free of smut; the other 3 gave over 85 per cent infection. Therefore, at least 3 of these normal  $F_3$  plants were susceptible and had escaped infection, and the assumption that all  $F_3$  progenies giving over 50 per cent infection were descended from genetically susceptible  $F_2$ 's is probably a correct one.

II. Survivors of 7  $F_3$  progenies which had given between 5.5 and 23.5 per cent infection were tested as to their reaction in the  $F_4$  generation:

3 $F_4$ families gave from	50–100 per cent infection
21 $F_4$ families gave from	5–50 per cent infection
16 $F_4$ families gave	0 per cent infection

The first 3 represented parental  $F_3$  plants which had escaped infection. The other two groups, resistant and segregating, were represented in every set of  $F_4$  families descended from a single  $F_3$  progeny. The segregating  $F_4$  families were considerably less than 50 per cent infected. They averaged 17.8 per cent, not far from the 18.8 per cent average for  $F_3$  segregating families nor the 20.9 per cent obtained for the  $F_2$  generation, both in the same year. These results tend to confirm the interpretations already given.

*F<sub>3</sub> generation of Dawn Kafir × Dwarf Yellow Milo.*  $F_3$  progenies of 30 uninoculated  $F_2$  plants were inoculated with *Sph. Sorghi*, and grown in 1934 under germination conditions which were very favorable for the production of smut. The distribution in 5 per cent infection groups is shown in figure 2, C. The 13 progenies in the 1–50 per cent group averaged 16.9 per cent infection, while 25 per cent of the  $F_2$ 's grown in the same year were smutted. The 7 progenies in the 50–100 per cent group averaged 69.6 per cent infection, a control row of Dawn Kafir 70.0 per cent. Dwarf Yellow Milo produced no smut. This figure is not essentially dissimilar to figure 2, B and, although the numbers are small, the distribution is highly



suggestive of a 1:2:1 ratio of resistant, segregating, and susceptible progenies.

*Reaction to Sphacelotheca cruenta*

*F<sub>1</sub> Generation.* Nineteen *F<sub>1</sub>* plants of the same milo hybrids were inoculated with *Sph. cruenta* and none were infected.

TABLE 4

*Infection results with F<sub>2</sub> plants and parental varieties of hybrids between Dwarf Yellow Milo and susceptible varieties, inoculated with Sphacelotheca cruenta*

HYBRID	YEAR	F <sub>2</sub> PLANTS			SUSCEPTIBLE PARENTAL VARIETIES		
		NO. PLANTS	NO. INF.	PER CENT INF.	NO. PLANTS	NO. INF.	PER CENT INF.
Dakota Amber Sorgo×*Dwarf Yellow Milo	1931	88	38	43.2	17	14	82.3
	1932	92	10	10.9	19	18	94.7
	1934	—	—	—	36	34	94.4
	1935	34	11	32.3	69	56	81.2
	Total	214	59	27.5	141	122	86.5
Shallu×Dwarf Yellow Milo	1934	57	27	47.4	24	22	91.6
	1935	36	24	66.6	48	39	81.3
	Total	93	51	54.8	72	61	84.7
Dwarf Yellow Milo×Shallu	1934	69	39	56.5			
	1935	34	7	20.5			
	Total	103	46	44.7			
Dawn Kafir×Dwarf Yellow Milo	1931	87	13	14.9	21	6	28.5
	1932	109	4	3.7	49	7	14.3
	1935	22	1	4.5	79	53	67.1
	Total	218	18	8.3	149	66	44.2
Dwarf Yellow Milo×Dawn Kafir	1934	73	26	35.6			
	1935	11	1	9.0			
	Total	84	27	32.1			

\* 242 plants of Dwarf Yellow Milo were grown (1931-1935) and one plant was infected (1934).

*F<sub>2</sub> Generation.* Results are recorded in table 4. Some data obtained by Reed (unpublished) may also be mentioned. In a year when the susceptible parent gave 37.5 per cent infection and the resistant parent was free

of smut, he found that 6.0 per cent of the  $F_2$  plants of the hybrid Dakota Amber Sorgo  $\times$  Dwarf Yellow Milo were infected. Inoculating 106  $F_2$  plants of Dawn Kafir  $\times$  Dwarf Yellow Milo with *Sph. cruenta*, he obtained 7.5 per cent infection, 27.3 per cent for the susceptible parent, and no infection for Dwarf Yellow Milo. In the present investigations,  $F_2$  infection percentages for the first of these hybrids were considerably higher, ranging from 10.9 to 43.2 per cent and averaging 27.5 per cent. For the second hybrid the average infection percentage was about the same as obtained by Reed, but for its reciprocal as high as 35.6 per cent infection occurred. Infection results with the susceptible parents were also correspondingly higher. For the Shallu-Dwarf Yellow Milo hybrids a maximum of 66.6 per cent infection occurred and both hybrids averaged over 40 per cent infection for the  $F_2$  generation.

These results are in distinct contrast to those of the *Sph. Sorghi* series, where 25.0 per cent infection in the  $F_2$  generation was the highest obtained for any hybrid in any year; this despite the fact that the susceptible parents were consistently more heavily infected in the *Sph. Sorghi* series than they were in the *Sph. cruenta* series. With this in mind it is highly probable that these same hybrids which, when inoculated with *Sph. Sorghi*, show segregation of a dominant factor for resistance; when inoculated with *Sph. cruenta*, show segregation of a dominant factor or factors for susceptibility. Reaction to the two smuts may depend upon different sets of factors, or it is possible that the factor which influences the behavior of these hybrids toward *Sph. Sorghi* may also influence their behavior toward *Sph. cruenta*, but in a reverse manner.

*F<sub>3</sub> generation.* For the hybrid, Dakota Amber Sorgo  $\times$  Dwarf Yellow Milo, 38  $F_3$  progenies from uninoculated  $F_2$  plants were grown in 1935. The seeds were taken from the same  $F_2$  plants from which  $F_3$  progenies inoculated with *Sph. Sorghi* were grown. The class distribution for this parallel series of  $F_3$  families inoculated with the loose smut is given in figure 2, D. The distribution suggests a 1:2:1 ratio, but it is obvious that this distribution is quite different from that of these same progenies when inoculated with *Sph. Sorghi* (fig. 2, B). The break between the resistant and segregating groups, and between the segregating and susceptible groups, is not as definite as it was in the *Sph. Sorghi* series. The largest number of segregating progenies to occur in any 5 per cent range came in the 30-35 per cent class, the average for all segregating progenies being 27.8 per cent; in the *Sph. Sorghi* series the largest number came in the 15-20 per cent class, the average for all segregating progenies being 18.8 per cent. Inoculated with *Sph. Sorghi*, hybrids between Milo and susceptible varieties, therefore, show a clear-cut segregation of resistant, segregating and

susceptible progenies, indicating that resistance may be governed by a single factor; inoculated with *Sph. cruenta* they do not show clear-cut segregation, indicating that reaction to this smut may be governed by more than one factor.

Literature cited is listed in Part II.

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## Factors affecting the method of branching in *Ailanthus altissima*

P. A. DAVIES AND E. W. THEISS

(WITH ONE TEXT-FIGURE)

The indefinite growth habit, so unusual in trees, is characteristic of *Ailanthus altissima* Swingle. Indefinite growth habits produce varying methods of branching. The different branching patterns in *Ailanthus* may be collected into two types: normal and abnormal. The normal method of branching is forked and irregular, with shoots developing at varying distances from the tip of the mother stem. The large pithy area in the center of the mother stem is not continuous with the pith of the branch; an intervening area is occupied by the wood. The abnormal method of branching appears at the apex of the shoots, and is fan-shaped and flattened.<sup>1</sup> The pith of the mother shoot is continuous with the pith of the branches and no intervening areas of wood appear (cf. Davies, 1936).

Methods of branching depend upon shoot growth. In any season, the normal shoot growth in *Ailanthus* is of two types: (1) short spur-like shoots which are rarely more than eighteen inches long and (2) long shoots. Keeler (1900) has reported shoots up to five feet in length. Davies (1936) has found shoots up to sixteen feet in length. The spur-like shoots are found on older trees, which because of extension growth, produce many but short shoots. The spur-like shoots on the upper part of the tree end in flower panicles. The long shoots occur on young rapidly growing trees, which produce few shoots, often only one, and these never terminate in flower panicles. The abnormal method of branching, when it is present, appears at the apex of the rapidly growing shoots.

Shoots in the normal method of branching arise from buds which developed the previous season. These buds form in the axils of the leaves, so the position of the leaves on the stem determines the position of the shoots. The abnormal branching pattern occurs at the apex of rapidly growing shoots and its growth and position are not dependent on bud formation of the previous season but is the result of an abnormal distribution of leaves on the shoot of the current season's growth. The positions of the shoots in both normal and abnormal branching methods depend on leaf position; the normal on leaf position of the previous season's growth and the abnormal on leaf position of the current season's growth. An understanding of leaf position is important in understanding the branching pattern. The normal leaf arrangement or system in *Ailanthus* is eight-

<sup>1</sup> Representatives of the abnormal method of branching are not abundant. The writers have found 271 cases of this method of branching.

ranked. The angular divergence of the leaves is  $135^\circ$  or three-eighths of a circumference. In such an arrangement, with the completion of the third revolution, leaf number nine is in position in line with leaf number one. In the abnormal branching pattern no such arrangement occurs. The arrangement corresponds to the position of the first abnormally placed leaves on the stem. If the leaves occur in opposite groups on the stem, opposite growing centers result. At the stem develops, it flattens. The intervening areas between the growing centers split, resulting in the abnormal branching pattern. Shoots arising from buds which appear in the axils of the abnormally placed leaves have the normal three-eighths leaf arrangement, so it is the normal and not the abnormal leaf arrangement which is important in determining the continuous branching pattern.

The shoots do not develop terminal buds, so all elongation depends upon the development of axillary buds. The maximum potential branch development on each stem is determined by the number of leaves. The shoots may vary from short spur-like shoots having as few as two leaves to very long shoots having as many as forty-eight leaves. If all the buds developed into shoots, the normal shoot arrangement on the mother stem would be as symmetrical as the normal leaf arrangement; but not all the buds develop, so the branching is never complete.

Figure 1 gives the relation of the number of shoots which developed on the mother stem to the number of buds which began activity. In this study counts were made on two successive years. The first season's count (solid line) was on 225 stems selected at random from different areas. The curve shows that 24.9 per cent developed only one shoot; 41.8 per cent, two shoots; 24.4 per cent, three shoots; 6.7 per cent, four shoots; and the remainder produced five shoots or more each. The number of shoots developed on the mother stem varied from one to eight, with an average of  $2.22 \pm .19$ . The second season's count (broken line) consisted of 436 mother stems selected at random. The curve shows that 23.6 per cent developed only one shoot; 35.3 per cent, two shoots; 28.7 per cent, three shoots; 7.8 per cent, four shoots; 1.8 per cent, five shoots; and one stem developed six shoots. The number varied from one to six shoots, with an average of  $2.27 \pm .14$  for each mother stem. The mode for both curves is 2. The results show a close seasonal correlation in the shoots which developed on the mother stems. It is evident that less than three shoots is sufficient to maintain the shoot balance on the mother stem.

Does the number of buds which begin development on the mother stem influence the number of shoots which finally develop? In order to determine if such a relation was active, counts were made on the number of buds which began development on 200 stems selected at random from

five localities. The curve (dotted line) in figure 1 shows that less than 2 per cent of the stems had as few as 7, 8, or 9 developing buds each, while the greatest percentage had from 12 to 16 developing buds each. The data (fig. 1) show that no direct relation is evident between the number of buds which begin activity in the spring and the number of shoots which finally develop.

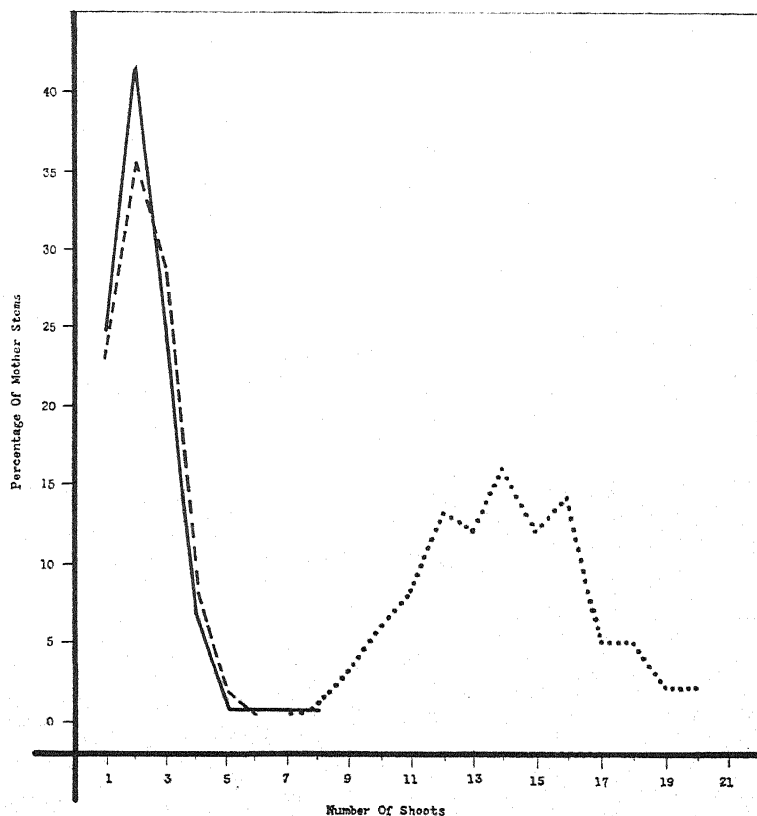


Fig. 1. Shows the percentage of mother stems producing varying numbers of shoots. The heavy line curve shows the relation on 225 mother stems after the shoot growth was complete. The broken line curve shows the same relation on 436 mother stems studied one year later. The dotted line curve shows the relation of the number of buds which began development on 200 mother stems.

As extension growth is the result of axillary bud development, the question arises, does the distance from the apex at which the buds develop determine the number of branches? Studies on 225 and 436 stems made on successive years show that the average bud position from which the uppermost shoot developed was  $9.15 \pm .68$  and  $4.38 \pm .11$  respectively. These

data compared with the data given in figure 1 indicate that, except for possibly the most apical bud, the position at which the uppermost bud develops does not influence the number of shoots which develop.

The shoot position on the average stem indicates that there are a number of buds above and below the shoot growth that fail to develop into shoots. Observations show that buds vary in size and shape. Is there a correlation between size or shape and the maturity of the buds (position on the mother stem at which shoots develop)? Measurements of the buds on 100 stems, chosen at random after leaf fall, show that the size of the bud, except for an occasional tiny bud near the apex, is proportional to the diameter of the supporting structure. On any individual stem, although there is a gradual change in shape from upper narrow to lower broad buds, the average shows that the greater percentage of the buds in positions 6 to 10 from the apex were the larger. Are these buds more mature than the smaller buds above and below them? To test this, 120 stems of varying length and diameters were selected at random after leaf fall but before freezing weather appeared. These were placed in a moist chamber at 30° C. with the cut ends in water. Of the 120 tested, 114 or 95 per cent showed upper bud development. The results show that when forced in a moist chamber the size and shape of the buds are no criteria of bud maturity, for, except in the exceptional case of tiny buds, buds in any position may be forced into development in a moist chamber by removing that portion of the stem above them. Failure of buds in certain positions on the stem to develop under natural conditions is due to factors other than size, shape, or maturity of the buds.

The failure of bud development below the shoots can be explained by the hormone theory of bud inhibition. Reviews on the experimental methods and results in bud inhibition studies are given by Snow (1932), Thimann (1935), Went (1935), and Boysen Jensen (1936). The results show that the upper developing buds produce an inhibiting hormone which is transported basically inhibiting lower bud development.

Although 95 per cent of the stems collected before freezing and forced into development showed upper bud development, 100 stems taken in the spring before bud development and placed under the same forcing conditions showed only 54 per cent upper bud development, a loss of 41 per cent. This loss of upper bud development indicates that the supporting tissue failed to mature sufficiently and was winter killed. Many of the tips were turning brown and were brittle when the stems were cut for the experiment. Eustace (1905) has shown for fruit trees and Farmer (1918) for young ash and sycamore trees that failure of fall ripening of the wood causes winter killing and failure of bud development on these dead areas.

Observations in the field after the last spring freeze showed that many of the upper buds had begun to develop and were killed by late spring freezing. A later count (at the time when shoot dominance was well established) showed only 6 per cent of the stems had upper shoot development. These observations are in agreement with those of Eustace (1905) and Wiggans (1919) for fruit trees and Farmer (1918) for ash and sycamore trees, that low temperatures after growth has actually begun in the buds is destructive to the buds and their supporting tissues. The late spring freezing accounts for the difference between 41 per cent of upper bud development obtained in the spring before bud activity and the 6 per cent which developed after the last freeze.

#### SUMMARY

Factors affecting the method of branching in *Ailanthus altissima* in this region are: (1) abnormal leaf arrangements, (2) lack of terminal bud formation, (3) dominating influence of a few shoots, (4) winter killing of the upper part of the shoot due to lack of maturity, and (5) late spring freezing.

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## INDEX TO AMERICAN BOTANICAL LITERATURE

1933-1937

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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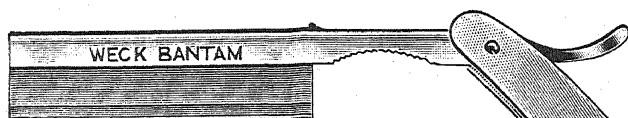
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## Inheritance of resistance to the loose and covered kernel smuts of sorghum

### II. Feterita hybrids<sup>1</sup>

D. ELIZABETH MARCY

The reaction of sorghum varieties and hybrids to the covered smut, *Sphacelotheca Sorghi*, and the loose smut, *Sphacelotheca cruenta*, has been recently reported (Marcy, 1937). The varieties Dwarf Yellow Milo and Feterita were found to be resistant, Dwarf Yellow Milo entirely so under all conditions, but Feterita manifesting effects of infection typified by the production of blasted heads, when the seedling environment was very favorable for infection. Crosses were made between these two resistant varieties. When the hybrids were inoculated with the covered smut, infected plants occurred, indicating that Feterita and Dwarf Yellow Milo possessed different factors for resistance; when inoculated with the loose smut all hybrid plants were normal, indicating that the two varieties had in common one factor for resistance to this smut.

Crosses were made between resistant and susceptible varieties, in the first series Dwarf Yellow Milo and in the second, Feterita, being used as the resistant parent. Infection results for the Dwarf Yellow Milo hybrids have already been discussed. Reaction to the covered smut was found to be governed by a single dominant factor for resistance; reaction to the loose smut apparently was influenced by more than one factor, susceptibility being incompletely dominant.

The present report considers hybrids between Feterita and susceptible varieties. Two strains of Feterita were used. The crosses are as follows:

Feterita 182 × Sumac Sorgo  
Dakota Amber Sorgo × Feterita 182  
Shallu × Feterita 182  
Dawn Kafir × Feterita 12 and reciprocal

The first and last crosses were made by Dr. George M. Reed and F<sub>1</sub> heads were available in his laboratory. The methods employed are entirely like those already outlined.

#### *Reaction to Sphacelotheca Sorghi*

*F<sub>1</sub> generation.* Ten out of 18 F<sub>1</sub> plants of crosses between Feterita and the susceptible varieties, Dakota Amber Sorgo, Dawn Kafir and Shallu, were smutted. Results were similar when either strain of Feterita was used, suggesting the dominance of susceptibility.

<sup>1</sup> Brooklyn Botanic Garden Contributions No. 76.

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*F<sub>2</sub> generation.* Infection data for the four Feterita hybrids and the parental varieties are given in table 1. Percentages of infection have been based on the number of typically smutted plants, excluding plants exhibiting the Feterita type of infection, in order to place data for all five years on a comparable basis.

TABLE 1

*Infection results with F<sub>2</sub> plants and parental varieties of hybrids between Feterita and susceptible varieties, inoculated with Sphacelotheca Sorghi*

HYBRID	YEAR	F <sub>2</sub> PLANTS			SUSCEPTIBLE PARENTAL VARIETIES		
		NO. PLANTS	NO.* INF.	PER CENT INF.	NO. PLANTS	NO. INF.	PER CENT INF.
**Feterita 182×Sumac Sorgo	1931	169	58	34.3	23	10	43.4
	1932	190	59	31.1	169	122	72.2
	1933	87	52	59.8	56	23	41.1
	1934	53	31	58.5	103	97	94.2
	1935	12	6	50.0	18	13	72.2
	Total	511	206	40.3	369	265	71.8
Dakota Amber Sorgo ×Feterita 182	1934	64	44	68.8	112	109	97.3
	1935	54	26	48.2	45	37	82.2
	Total	118	70	59.3	157	146	92.9
Shallu × Feterita 182	1934	65	51	76.9	33	33	100.0
	1935	5	4	80.0	30	29	96.6
	Total	70	55	78.6	63	62	98.4
**Feterita 12×DawnKafir	1931	91	33	36.3	42	20	47.7
	1932	55	10	18.2	36	6	16.6
	1933	67	43	64.2	36	24	66.6
	1934	28	15	53.5	142	132	93.0
	1935	34	16	47.0	51	44	86.3
	Total	275	117	42.5	307	226	73.6
Dawn Kafir×Feterita 12	1931	168	59	35.1			
	1932	112	35	31.3			
	1933	94	59	62.8			
	1934	73	49	67.1			
	1935	77	42	54.5			
	Total	524	244	46.5			

\* Infected plants include only those which were typically smutted.

\*\* From 1931 to 1935, 677 plants of Feterita 182 were grown, and 0.9 per cent were typically smutted, but none of the 141 plants of Feterita 12 were smutted.

The hybrid Feterita 182  $\times$  Sumac Sorgho has been investigated more thoroughly than any other. The reaction of the  $F_2$  generation to *Sph. Sorghi* over a period of seven years (1924–1930) has been ascertained by Reed (1930, and unpublished data). Growing a total of 2071  $F_2$  plants, he obtained from 28.0–68.5 per cent infection, averaging 43.9 per cent for the hybrid; 31.4–86.1 per cent averaging 49.8 per cent for the susceptible parent, and one smutted plant out of a total of 569 of the resistant parent. Data obtained by the writer during the years 1931–1935 were entirely similar. Infections with the hybrid were as high as 59.8 per cent but averaged only 40.3 per cent, and with the susceptible parent as high as 94.2 per cent, but averaged only 71.8 per cent.

Infection percentages for the varieties Dakota Amber Sorgho and Shallu were somewhat higher. Only one plant out of 63 of Shallu was normal. Likewise the hybrids involving these varieties as parents were heavily smutted, the first averaging 59.3 per cent and the second 78.6 per cent infection.

Feterita 12  $\times$  Dawn Kafir gave as high as 64.2 per cent infection in the  $F_2$  generation and the reciprocal hybrid as high as 67.1 per cent. Since these hybrids were grown in years when the environment was unfavorable for high infections as well as in years when it was favorable, the average infection percentages were low, as were those of  $F_2$  generation plants of Feterita 182  $\times$  Sumac Sorgho. Inoculated  $F_2$  plants of the same hybrids, grown by Reed (1927, 1929, and unpublished data) gave from 20.2 to 45.4 per cent infection averaging 36.4 per cent for Feterita 12  $\times$  Dawn Kafir and from 31.4 to 52.4 per cent averaging 46.9 per cent for the reciprocal. From 46.8 to 65.7 per cent averaging 62.4 per cent was obtained for Dawn Kafir, and 2 plants out of a total of 191 of Feterita 12 were infected. Therefore, in respect to *Sph. Sorghi*, infection results were similar for all these hybrids regardless of the strain of Feterita involved. Reed's results with the Dawn Kafir and the Sumac Sorgho hybrids led him to conclude that susceptibility was dominant and probably governed by a single factor. The increased infection percentages obtained by the writer in 1934 and 1935, particularly with the Shallu hybrids, leave little doubt but that there is segregation of a major dominant factor for susceptibility in Feterita hybrids.

*Blasting among Feterita hybrids.* The same pathological symptoms noted in Feterita in 1934 and 1935, characterized by blasted heads, appeared in the Feterita hybrids for those years. It is necessary now to reclassify the plants of the Feterita group of hybrids grown in 1934 and 1935 into normal, blasted, and typically smutted groups. This has been done in table 2. In all but the Feterita 12 hybrids the number of blasted heads was greater than the number of normal.

There were grown, in the  $F_3$  generation, progenies of the hybrid Feterita 12  $\times$  Dawn Kafir and its reciprocal, and in the  $F_3$  and  $F_4$  generations, progenies of the hybrid Feterita 182  $\times$  Sumac Sorgo, approximately 20 plants per progeny, except as noted.

$F_3$  generation of Feterita  $\times$  Sumac Sorgo.  $F_3$  data, for two crosses between Feterita and Sumac Sorgo, were more extensive than for any other hybrid, and, since results were obtained in 1932 and also in 1934, opportunity was given for a comparison of infection reactions under different environal conditions.

TABLE 2

*F<sub>2</sub> segregation of smutted, blasted and normal plants in the 1934 and 1935 series of Feterita hybrids, inoculated with Sphacelotheca Sorghi*

HYBRID	NO. PLANTS	NO. TYPICALLY SMUTTED	NO. BLASTED	NO. NORMAL	PER CENT TYPICALLY SMUTTED	PERCENTAGE OF NON- SMUTTED, BLASTED
Feterita 182 $\times$ Sumac Sorgo	65	37	18	10	56.9	64.2
Dakota Amber Sorgo $\times$ Feterita 182	118	70	38	10	59.3	79.2
Shallu $\times$ Feterita 182	70	55	11	4	78.6	73.3
Feterita 12 $\times$ Dawn Kafir	62	31	13	18	50.0	41.9
Dawn Kafir $\times$ Feterita 12	150	91	26	33	60.7	44.1
Feterita 182	350	5	140	205	1.4	41.4
Feterita 12	80	0	15	65	0	18.8

$F_3$  progenies from each of 98 uninoculated  $F_2$  plants were tested for their reaction to *Sph. Sorghi*. Twenty-five of these, with 60–70 plants per progeny, were grown by Reed in 1925 and the infection data, hitherto unpublished, are included here; 73, with 20–30 plants per progeny, were grown under similar conditions by the writer in 1932. The distribution in percentage classes for both years (fig. 1A) is similar, a wide range of infection percentages being represented without any clear-cut break between resistant, segregating, and susceptible groups. There were only 13 completely resistant progenies out of the 73 grown in 1932, and only 2 out of the 25 grown in 1925, when the number of plants per progeny was larger. But if progenies giving up to 5 per cent infection, as Feterita sometimes does, are considered resistant, those giving from 5 to 50 per cent, segregating, and those giving over 50 per cent, susceptible, the fit to a 1:2:1 ratio is very good for both 1925 and 1932 data. However, since  $F_2$  results in later years have indicated the dominance of susceptibility, progenies in the segregating group should have been more than 50 per cent infected.

Instead, most of these came in the 25–45 percentage classes, averaging only 27.3 per cent infection in 1925 and 28.7 per cent in 1932. Infection

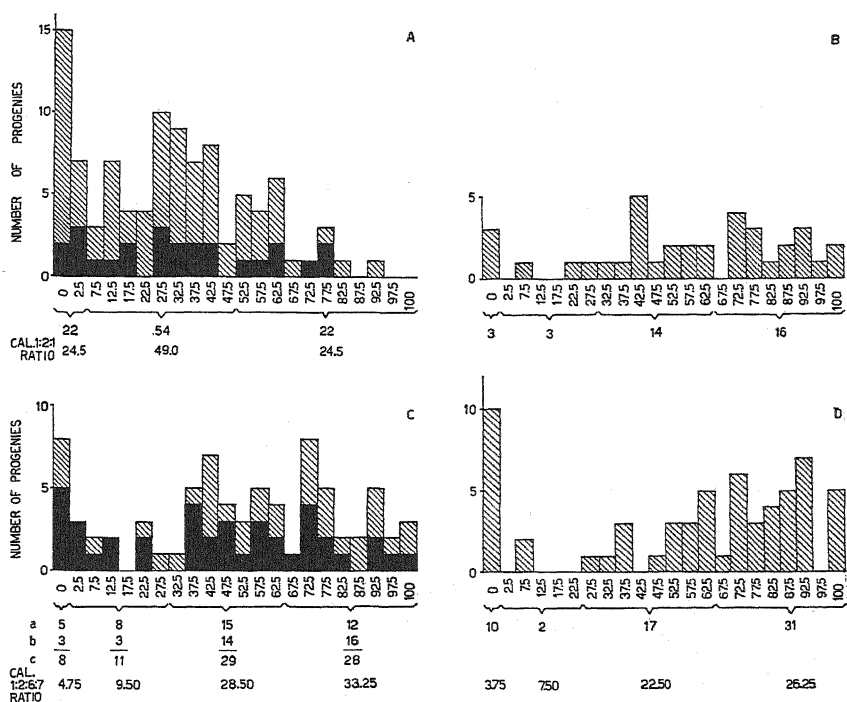


Fig. 1. Distribution of  $F_2$  progenies into 5 per cent classes on the basis of infection with the covered smut, *Sphacelotheca Sorghi*.

A—C Feterita  $\times$  Sumac Sorgo.

A—Solid areas—Seedlings germinated in sand with 20 per cent moisture ( $H_2O$ )—1925.

Shaded areas—Seedlings germinated in sand with 30 per cent moisture ( $H_2O$ )—1932.

B—Seedlings germinated in sand with 10 per cent moisture (2 per cent sucrose solution)—1934.

C—Solid areas—Distribution of 40  $F_2$  progenies reconstructed on the basis of the infection reactions of their  $F_4$  descendants (10 per cent moisture, sucrose)—1934.

Shaded areas—Distribution of  $F_2$  progenies represented in B.

D—Feterita  $\times$  Dawn Kafir and the reciprocal hybrid. (10 per cent moisture, sucrose)—1934.

percentages for the  $F_2$  generation were also low for these years, 43.7 per cent in 1925 (Reed, 1930) and 31.1 per cent in 1932. Such results seem to indicate the dominance of resistance rather than susceptibility. Undoubt-



edly the failure to obtain a full quota of infected plants with Sumac Sorgo in 1925 and 1932 (40.2 and 72.2 per cent respectively) partly accounts for the small proportion of hybrid plants infected. Apparently, during these years, the environment was such that many genetically susceptible plants escaped infection. The fact that under these conditions there were so few resistant progenies makes it clear that resistance in this cross is affected by more than one factor. The tendency of the progenies to fall in certain percentage groups rather than others, suggests that a few rather than many factors are involved.

With these points in mind two different approaches were made toward the clearing up of this problem. The first was to grow more  $F_3$  progenies under an environment more favorable for infection, the second was to grow  $F_4$  progenies from certain survivors of these  $F_3$ 's and reconstruct their behavior from  $F_4$  results.

*Additional  $F_3$  data under better enviroinal conditions.* An infection environment more favorable than that provided in 1932 was discovered in 1934 and an additional set of 36  $F_3$  progenies from uninoculated  $F_2$  plants was germinated under these enviroinal conditions. The distribution in percentage classes is given in figure 1B. The most striking difference between this figure and figure 1A is the very low proportion of progenies with zero or low infection percentages and the large proportion with very high infections. The results no longer suggest a 1:2:1 ratio.

*$F_4$  generation of *Feterita*  $\times$  *Sumac Sorgo*.* Another way of getting at this problem, i.e., to reconstruct  $F_3$  data from  $F_4$  results, was also accomplished in 1934. Survivors of 40 of the 1925 and 1932  $F_3$  progenies were grown in the  $F_4$  generation in 1933 and 1934 under conditions conducive to high infections. The distribution of the  $F_3$  progenies from which these  $F_4$ 's were grown covered the entire range of percentage classes. There was a total of 331  $F_4$  families, the  $F_3$  parent plants of which had all survived inoculation. Data may be briefly summarized as follows:

I. The survivors of 10  $F_3$  progenies which were more than 50 per cent smutted were grown in the  $F_4$  generation. Forty-four of the 57  $F_4$  families tested gave over 50 per cent infection, many of them over 80 per cent. Of the rest, giving less than 50 per cent infection, 4 were entirely resistant, 1 of them breeding true for resistance in the  $F_5$  generation. All  $F_3$  progenies giving over 50 per cent infection cannot, therefore, in this cross, be classified as homozygous susceptibles.

II. Six smut-free  $F_3$  progenies were tested in the  $F_4$  generation. Three produced only smut-free  $F_4$  descendants out of a total of 38 families grown, but 3 others each produced a few families containing from 11.1–66.6 per cent infected plants, 7 families altogether out of a total of 33 tested. All

the  $F_3$  progenies free of smut have not, therefore, been accurately classified as homozygous resistants.

III. An  $F_4$  family was grown from each of 26 survivors of 3  $F_3$  progenies which had given 1–5 per cent infection. None produced an entire quota of  $F_4$  families free of smut. A few of the resistant  $F_4$ 's were inoculated in the  $F_5$  generation and not all were found to breed true. It is possible, therefore, to grow  $F_3$  progenies from non-smutted  $F_2$  plants, and from the smut-free progenies among these to grow progenies in the  $F_4$  generation, and from the smut-free progenies among these to grow progenies in the  $F_5$  generation, and still have smutted plants appear. Thus it is evident that more than one factor is concerned with the inheritance of resistance in this hybrid.

IV.  $F_3$  progenies which gave from 5 to 50 per cent infection may be grouped in several categories.

(1) Six  $F_3$  progenies gave rise to 44  $F_4$  families all with over 40 per cent infection, and therefore probably belonged to the homozygous susceptible group.

(2) One  $F_3$  progeny with 12.5 per cent smutted plants produced all normal  $F_4$  families.

(3) The rest of the  $F_3$  progenies in the 5–50 per cent group were found to be definitely segregating, but the infection reactions of their  $F_4$  descendants indicated that they represented three distinct segregating groups:

- (a) One group of 3  $F_3$  progenies produced 9 families free of smut and 14 which gave from 54.5 to 100 per cent infection, which suggests that their  $F_2$  ancestor may have contained a single dominant factor for susceptibility.
- (b) A second group of 2  $F_3$  progenies produced 4  $F_4$  families free of smut and 12 giving from 7.5 to 40 per cent infection, which suggests that their  $F_2$  ancestor may have contained a single dominant factor for resistance.
- (c) A third group of 9  $F_3$  progenies gave rise to 87  $F_4$  families with infection percentages ranging all the way from 0 to 100 per cent, suggesting that the  $F_2$  ancestors of these families contained more than one factor influencing reaction to *Sph. Sorghi*, and that possibly the families in groups 1 and 2 represent the separate segregation of each of these factors.

*Reconstruction of  $F_3$  data from  $F_4$  results.* An  $F_3$  plant which produced an  $F_4$  progeny giving more than 50 per cent infection must have itself been an escape. By considering these additional  $F_3$  plants susceptible, the  $F_3$  infection percentages of the 40 families from which  $F_4$  progenies had been grown can be reconstructed, and a more accurate classification of these families obtained. The new class distribution of  $F_3$  progenies, based on these reconstructed data, is shown in figure 1C (black areas and a). Since

not all survivors of an  $F_2$  family were grown, percentages of infection should be at least as high as represented here. Two percentage groups now stand out with clearness, the first including from 0 to 25 per cent infection, the second from 35 to 100 per cent. Those which gave from 0 to 25 per cent infection represent two groups, one resistant and the other segregating, with resistance dominant, and those which gave from 35 to 100 per cent infection also probably represent two groups, one susceptible and the other segregating, with susceptibility dominant. It is not possible to tell whether the line of demarcation between these two latter groups occurs at 65 or 85 per cent. If this figure is compared with figure 1B, it can be seen that the distribution is approximately the same for both series. Combining the data (shaded areas, and c), the break between the segregating group giving low infections and the segregating group giving high infections seems to occur at about 30 per cent, and the break between the segregating group giving high infections and the susceptible group, at about 65 per cent.

The fact that there was a definite group of progenies with low percentages of infection, along with the fact that the number of resistant progenies was extremely small and did not all breed true in subsequent generations, indicates the segregation of a dominant factor for susceptibility which will be termed S, epistatic to or inhibiting the expression of a factor for resistance which will be termed B. This B factor is presumably from Feterita and accountable for the blasting prevalent among non-smutted plants.

The independent assortment of these two factors would take place as follows:

$F_2$ genotypes	Segregation of $F_2$ progenies
1 SSBB	All smutted
2 SSBb	All smutted
2 SsBB	3:1 smutted to blasted
4 SsBb	13:3 smutted to blasted
1 SSbb	All smutted
2 Ssbb	All smutted
1 ssBB	All blasted
2 ssBb	3:1 blasted to smutted
1 ssbb	All smutted

It is impossible, in this work, to separate the group segregating in a 3:1 ratio (75 per cent infection) from the group segregating in a 13:3 ratio (81.75 per cent infection). If these two groups are combined, the resistant, segregating resistant, segregating susceptible, and susceptible groups should occur in a 1:2:6:7 ratio. The agreement of these data with this

ratio as calculated (fig. 1C) is fairly close. The last two groups, comprising 57 progenies, would be expected to smut in the  $F_2$  generation, the first two, comprising 19 progenies, to remain smut free, the two groups bearing the relationship of 13:3 or, on the basis of 76 progenies, 61.75:14.25. The agreement is seen to be fair, the excess progenies occurring, as would be expected, in the zero or lower percentage groups, since some susceptible plants were escaping infection.

In the foregoing discussion only those plants which were typically smutted were considered infected. The non-typically smutted plants, whether normal or blasted, have been grouped together. According to the hypothesis given, no plants should occur which were genetically more resistant than Feterita. The  $F_2$  data support this for, in most of these hybrids, more than half the non-smutted plants were blasted. This is all that would be expected, since Feterita itself produced only about 50 per cent blasted plants. Only 3 of the 1934  $F_2$  progenies, containing more than 5 non-smutted plants, were free of blasted heads. They were also present in most of the  $F_4$  progenies grown in 1934. It seems likely that all non-smutted plants contained the Feterita factor.

It has been assumed that high infections in the hybrid in 1934 were entirely due to the more complete expression of the factor for susceptibility brought in by Sumac Sorgo, disregarding the fact that the 1934 environment also weakened the effect of the Feterita factor for resistance. It is probable that the infection of hybrid plants containing both the S and B factors may depend not only upon the influence of environment on the expression of the S factor, as assumed earlier, but also upon its influence on the capacity of the B factor to inhibit infection. If B were completely inhibiting infection and therefore epistatic to S, a 3:1 ratio of resistant to susceptible plants would occur. If its inhibiting effect was eliminated, S would be epistatic to B, and a 13:3 ratio of susceptible to resistant plants would occur. In 1932, results with hybrids approximated the first ratio, in 1934 the second. Apparently the plants with both the S and B factors were the ones which "escaped" infection in 1932, the complete epistasis of S over B existing only when some effect of the environment counteracted the effect of the B factor entirely. It would have been too much to expect the 1932 and 1934 data to exactly coincide with the "end points" of this factor interaction, but the agreement is near enough to be convincing. Such results demonstrate that plants of the SB genotype are far more sensitive to enviroinal changes than plants of either the Sb (Sumac Sorgo) or sB (Feterita) genotypes.

It is obvious that between a set of enviroinal conditions which would completely eliminate the effect of the B factor and a set which would allow

for its complete expression, exist intermediate enviroal conditions under which the chances of a plant becoming smutted or remaining normal would be about equally divided, and would therefore be governed by extremely slight differences in environment. It is possible that plants with the genotype SSBb would be more likely to become infected than those with any of the other genotypes, since S is homozygous and B heterozygous. These, then, would be the first to change from resistant to susceptible, as the effect of B was weakened. Such a change would alter the 3:1 ratio to a 5:3 ratio of resistant to susceptible plants and 37.5 per cent infection rather than 25 per cent would occur in the  $F_2$  generation. The actual percentages obtained in 1925, 1931, and 1932 were 40.4 (Reed 1930), 34.3, and 31.1 per cent.

If an environment were supplied which weakened the effect of B even more,  $F_2$  plants possessing S and B in equal proportions would shift from the resistant to the susceptible group, and only those plants of the SsBB genotype would remain resistant. Susceptibility rather than resistance would now be dominant; the ratio of resistant to susceptible  $F_2$ 's would change from 5:3 to 5:11, and 68.75 per cent infection would be expected in the  $F_2$  generation. In 1933, 1934, and 1935, 59.8, 58.5, and 50 per cent infections were obtained. When the effect of the factor B has been completely eliminated, 81.75 per cent of the  $F_2$  plants would be expected to smut. Infections for this hybrid in the  $F_2$  generations were never quite that high, but 78.6 per cent was obtained for the hybrid Shallu  $\times$  Feterita.

In the change from the dominance of resistance to the dominance of susceptibility, the distribution of  $F_3$  progenies would also be altered. The numbers of segregating and non-segregating progenies would remain equal throughout, but the number of resistant progenies would decrease as the number of susceptible progenies increased, the ratio of homozygous resistant to homozygous susceptible progenies changing from 1:1 to 1:7. A comparison of figures 1A and 1C shows this to be true. Results recorded in figure 1A indicate 54 segregating progenies and 44 non-segregating, 22 resistant and 22 susceptible (theoretically 1:1); results recorded in figure 1C indicate 40 segregating progenies and 36 non-segregating, 8 resistant and 28 susceptible (theoretically 1:7).

It might be noted here that the distribution of  $F_3$  progenies in 1925 and 1932 (fig. 1A) is very like the  $F_3$  distribution for the hybrid between Dakota Amber Sorgo and Dwarf Yellow Milo in the *Sph. cruenta* series (Marcy, 1937), when Dakota Amber Sorgo was giving 81.2 per cent infection, much the same as Sumac Sorgo was giving with *Sph. Sorghi* in 1932. It seems a fair prediction that, were  $F_3$  progenies of the Milo hybrid in the *Sph.*

*cruenta* series grown again under more favorable conditions, results might simulate those obtained with this Feterita hybrid in the *Sph. Sorghi* series. It seems evident that Milo hybrids react toward *Sph. cruenta* as Feterita hybrids toward *Sph. Sorghi*, and that there may be the same type of factor interaction.

*F<sub>3</sub> generation of Feterita 12 × Dawn Kafir and reciprocal.* In 1934, 60 *F<sub>3</sub>* progenies, 30 of the hybrid, Feterita 12 × Dawn Kafir, and 30 of the reciprocal, all originating from uninoculated *F<sub>2</sub>* plants, were inoculated with *Sph. Sorghi*. Fifteen to twenty plants per progeny usually reached maturity. The infection reactions of the two hybrids were entirely similar, and the data have been combined (fig. 1D).

That the distribution of these progenies is similar to the distribution of *F<sub>3</sub>* progenies for the Feterita × Sumac Sorgho hybrid is obvious by comparing figure 1D with figure 1C, and suggests that the factors operative here are the same.

There is some doubt as to whether the progenies giving from 25 to 40 per cent infection belong with the segregating resistant group, for which their infection percentages are rather high, or with one of the segregating susceptible groups. At present they will be treated as belonging to one of the latter groups, since infection percentages are usually lower rather than higher than expectations. On this assumption, the agreement to a 1:2:6:7 ratio is fair for the susceptible groups, but very poor for the resistant groups. It is possible that if the resistant progenies were tested in the *F<sub>4</sub>* generation, as for the preceding hybrid, some of them would be found to belong to the segregating resistant group. The *F<sub>2</sub>* segregation, as interpreted from *F<sub>3</sub>* data, is very close to the expected 13:3 ratio, the actual ratio being 48:12, the expected ratio 48.75:11.25.

As for the preceding hybrid, all non-smutted plants should contain the factor for blasting. Only 2 progenies with more than 5 non-smutted plants were free of blasted heads. Feterita 12 in 1934 gave only 19.2 per cent blasted heads, so high percentages of blasted heads would not be expected to occur among any of the progenies.

This hybrid therefore is entirely like the preceding one in reaction to *Sph. Sorghi* and, like it, indicates the interaction of two factors, the one for susceptibility epistatic to the one for resistance.

#### *Reaction to Sphacelotheca cruenta*

*F<sub>1</sub> generation.* Seven *F<sub>1</sub>* plants of a cross between Feterita 182 and Dakota Amber Sorgho were all normal, but 14 out of 18 plants of Feterita 12 × Dawn Kafir and the reciprocal cross were smutted. Results with

crosses involving Feterita 182 indicated the dominance of resistance to *Sph. cruenta*, as for Milo crosses, while results with crosses involving Feterita 12 indicate the dominance of susceptibility.

TABLE 3

*Infection results with F<sub>2</sub> plants and parental varieties of hybrids between Feterita and susceptible varieties inoculated with Sphacelotheca cruenta*

HYBRID	YEAR	F <sub>2</sub> PLANTS			SUSCEPTIBLE PARENTAL VARIETIES		
		NO. PLANTS	NO. INF.	PER CENT INF.	NO. PLANTS	NO. INF.	PER CENT INF.
*Feterita 182×Sumac Sorgo	1931	87	2	2.3	18	1	5.5
	1932	201	3	1.5	112	55	49.1
	1934	—	—	—	49	20	40.8
	1935	28	3	10.7	17	1	5.8
	Total	316	8	2.5	196	77	39.3
Dakota Amber Sorgo ×Feterita 182	1934	66	6	9.1	36	34	94.4
	1935	40	4	10.0	69	56	81.2
	Total	106	10	9.4	105	90	85.7
Shallu×Feterita 182	1934	62	8	12.9	24	22	91.6
	1935	29	0	0	48	39	81.3
	Total	91	8	8.8	72	61	84.7
**Feterita 12×Dawn Kafir	1931	78	50	64.1	21	6	28.5
	1932	57	31	54.4	49	7	14.3
	1934	—	—	—	95	57	60.0
	1935	36	24	66.6	79	53	67.1
	Total	171	105	61.3	244	123	50.4
Dawn Kafir×Feterita 12	1932	114	34	29.8			
	1935	54	29	53.7			
	Total	168	63	37.5			

\* 500 plants of Feterita 182 were grown (1931-1935) and none were infected.

\*\* 21 plants of Feterita 12 were grown in 1931 and 4.7 per cent were infected; 18 plants in 1932 and none were infected, and 35 plants in 1935 and 17.1 per cent were infected.

*F<sub>2</sub> generation.* Data for the four Feterita hybrids inoculated with the loose smut are presented in table 3. F<sub>2</sub> plants of Feterita×Sumac Sorgo gave no higher than 10.7 per cent infection in any year, but Sumac Sorgo also gave low infection percentages. Reed (unpublished data), growing 415

plants of the hybrid, obtained 5.3 per cent infection, and 25.8 per cent for Sumac Sorgo. Feterita has been free of smut throughout. Dakota Amber Sorgo  $\times$  Feterita 182 and Shallu  $\times$  Feterita 182 gave infection percentages very little higher, even though a considerably larger proportion of the susceptible parent plants were smutted. The results indicate clearly that resistance to the loose smut was dominant.

In contrast to these hybrids, as high as 66.6 per cent infection was obtained for Feterita 12  $\times$  Dawn Kafir, and as high as 53.7 per cent for the reciprocal cross. Dawn Kafir, however, was not more heavily infected than the other susceptible varieties. Reed noted only 8.5 and 26.7 per cent infection for the same two hybrids, but Dawn Kafir was giving only 17.1 per cent infection. In their reaction to *Sph. cruenta*, therefore, the hybrids involving strain 12 of Feterita differed from those involving strain 182, but were similar to the hybrids between Dawn Kafir and Dwarf Yellow Milo, susceptibility being dominant. It has been noted earlier that the genotypes of these two strains of Feterita might differ. Data for these hybrids provide evidence in support of this point.

*F<sub>3</sub> generation of Feterita 182  $\times$  Sumac Sorgo.* Thirty-seven sister progenies of some of the  $F_3$  progenies inoculated with *Sph. Sorghi* in 1932 were inoculated with *Sph. cruenta* and also grown in 1932. Their percentage class distribution is as follows:

- 23 gave no infection
- 12 gave 5–50 per cent infection
- 2 gave 50–100 per cent infection

Therefore, out of a total of 37 progenies, 2 or 5.4 per cent might have been expected to smut if the  $F_2$ 's had been inoculated.  $F_2$ 's grown in 1932 actually gave 1.5 per cent infection. Feterita was free of smut and Sumac Sorgo 49.1 per cent infected.

*F<sub>4</sub> generation.*  $F_4$  families, with 18–30 plants per family, were grown from 24 of these  $F_3$ 's in 1934. Results may be summarized as follows:

I. Seventeen resistant  $F_3$  progenies were tested in the  $F_4$  generation. Only 8 of these (from which 96  $F_4$  families have been grown) were found to breed true for resistance. The other 9 each produced some  $F_4$  families with infected plants. For a total of 116  $F_4$  families 83 were free of smut, 28 gave from 1 to 50 per cent infection, and 5 from 50 to 100 per cent infection. Therefore not all  $F_3$  progenies free of smut were true breeding resistants.

II. Survivors of 3  $F_3$  progenies which had given 5.2, 14.4 and 22.2 per cent infection were tested in the  $F_4$  generation. Of the 26  $F_4$  families grown, 10 were uninfected, 14 gave from 1 to 50 per cent infection and two, 50 per cent or over, the latter probably representing  $F_3$  plants which had escaped



infection. It is probable that these  $F_3$  progenies represented a segregating group.

III. Thirty  $F_4$  families from 4  $F_3$  progenies which had given more than 35 per cent infection gave only high percentages of infection, 25 of them over 50 per cent, the other 5 between 30 and 50 per cent, none being entirely resistant. It is probable that these progenies represented a homozygous susceptible group.

*Reconstruction of  $F_3$  data from  $F_4$  results.* Data for these 24  $F_3$ 's tested in the  $F_4$  generation have been revised in the same way as for the *Sph.*

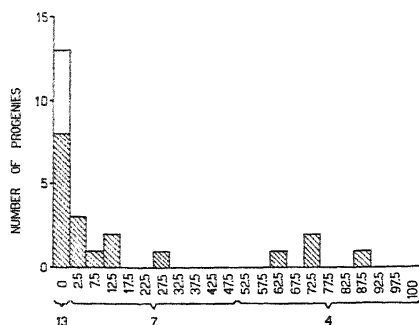


Fig. 2. Distribution of  $F_3$  progenies of the cross Feterita  $\times$  Sumac Sorgho into 5 per cent infection classes on the basis of infection with the loose smut, *Sphacelotheca cruenta*—reconstructed from infection reactions of their  $F_4$  descendants (10 per cent moisture, sucrose)—1934.

hypothesis, the  $F_2$  ratio of normal to smutted should be approximately 4:1. Here there were 20 progenies giving under 50 per cent infection and 4 over 50 per cent. Of the group giving below 50 per cent infection, two-fifths should breed true for resistance. Eight out of the 20 were found to do so. Although very close to expectations, the results are too meager to provide any proof of this hypothesis.

In order to determine whether there is any correlation between resistance to *Sph. Sorghi* and resistance to *Sph. cruenta*, larger numbers of progenies must be grown. So far it has been noted that all progenies resistant to *Sph. Sorghi* have also been free of smut when inoculated with *Sph. cruenta*.

No  $F_3$  data have been obtained for the hybrids between Dawn Kafir and Feterita.

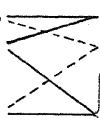
There is very clear-cut evidence here that reaction to the two smuts

*Sorghii* series, and the reconstructed distribution shown in figure 2. Thirteen progenies now come in the resistant class, only 8 of which, as stated, breeding true, 7 progenies in the 1-50 per cent group, and 4 progenies in the 50-100 per cent group. If the same factors governing reaction to *Sph. Sorghi* also govern reaction to *Sph. cruenta*, it is obvious that their effect is reversed. These results show that the factor for resistance is epistatic to the factor for susceptibility. They also indicate the presence of a second factor for resistance to which the factor for susceptibility is apparently epistatic. According to this three factor

depends upon the resistant variety brought into the cross. Susceptibility was dominant in the Milo crosses, resistance dominant in the Feterita 182 crosses when inoculated with *Sph. cruenta*; resistance was dominant in the Milo crosses, and susceptibility dominant in the Feterita 182 crosses when inoculated with *Sph. Sorghi*.

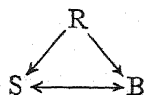
#### DISCUSSION

Three factors governing reaction to the covered smut have been postulated, R and B, factors for resistance, and S, a factor for susceptibility. Accordingly, it is suggested that the genotypes of the parental varieties may be as follows:

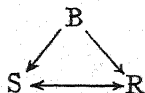
Variety	Genotypes	$F_2$ segregation— <i>Sph. Sorghi</i>	
Dwarf Yellow Milo	RRbbss		
Susceptible varieties	rrbbSS		3:1 Resistant to susceptible
Feterita	rrBBss		15:1 Resistant to susceptible
		13:3 Susceptible to resistant	
		or	
		3:1 Resistant to susceptible	

Ratios in the  $F_2$  generation, as deduced from  $F_3$  reactions, have been found to approximate those indicated. In crosses between Dwarf Yellow Milo and susceptible varieties, therefore, there is segregation of the factors R and S, the results demonstrating complete epistasis of R over S; in crosses between Dwarf Yellow Milo and Feterita, segregation of the factors R and B, the results demonstrating the complete epistasis of R over B; and in crosses between Feterita and susceptible varieties there is segregation of the factors S and B, the results demonstrating complete epistasis of S over B when one set of seedling enviroal conditions was supplied, but almost complete epistasis of B over S when another set of conditions was supplied.

The same hybrids, inoculated with the loose smut, showed quite the opposite reactions. In Feterita 182 crosses resistance was completely dominant, and in Milo crosses susceptibility was incompletely so. The factors governing reaction to *Sph. cruenta* may be the same as those governing reaction to *Sph. Sorghi*. The factor relationships would differ, however, and may be expressed diagrammatically as



for covered smut reactions and



for loose smut reactions.

The upper factor in each diagram is considered epistatic to each of the lower ones, and this relationship has been found to be a stable one, very little affected by changes in external environment. The two lower factors are potentially equal in their expression and, since they govern opposite reactions, the relationship between them is an unstable one, and the balance may be thrown one way or the other by changes in the external environment. For reaction to the loose smut this is still an assumption. For reaction to the covered smut it has been clearly demonstrated, by growing hybrids segregating for the S and B factors under differing, controlled environments.

This is a rather unusual case of epistatic factor relationship. The results illustrate, not the presence of a graded series of factors, differing in their potencies or cumulative in effect, but rather the interaction of balanced factors antagonistic in effect. Although not strictly analogous, these data are highly suggestive of the results of Goldschmidt (1928) and others, which have led to the postulate of "genic balance." It would be interesting to know how in the present investigations the environment can alter this balance. The crux of the problem lies in determining what the Feterita factor, B, specifically controls. No direct evidence is presented here, but, since the environment has been changed during the germination period only, the B factor must govern some aspect of initial infection. It is possible that it regulates some physiological process which acts as a barrier to the initial establishment of the fungus in the apical meristem, and that manipulation of enviroanal conditions has somehow curtailed that process. The infection of any plant would therefore depend on how completely the effect of the B factor was counteracted. When the environment was such as to make the odds about even, very slight fluctuations in external conditions, the heterozygous or homozygous state of the B factor, or even the slight variations which exist between plants which are genetically alike, would determine whether or not a plant were smutted or normal. Under such conditions plants with both the S and B factors would be extremely unstable. When the environment was such as to completely throw the balance one way or the other, slight fluctuations would not affect the resistance of a plant, and its reaction would be comparatively stable. Therefore hybrids grown at the extremes of enviroanal influence would give clear-cut segregation, while hybrids grown in intermediate environments would show a tendency for resistant, segregating, and susceptible groups to be ill defined. This type of interrelationship between factors explains why a cross between a resistant and a susceptible variety may give rise to hybrids which, even under similar enviroanal conditions, are more unstable in their infection reactions than the parents.

That this type of factor interaction may occur quite generally in relation to the inheritance of disease resistance is suggested by results obtained by Briggs (1930b) and Churchward (1931, 1932) for reaction of hybrids to bunt of wheat and by Reed (1932b) for loose and covered smuts of oats. Crosses made by Briggs between a hybrid selection possessing the Hussar factor alone and a susceptible variety, Little Club, gave  $F_2$  rows with infection percentages from 31.7 to 66, the lowest similar to those of the Feterita hybrids in 1932, the highest, to those obtained in 1934.  $F_3$  progenies also showed a distribution comparable to that of Feterita hybrids in 1932. Churchward, crossing Florence with susceptible varieties, obtained 45–69.6 per cent infection in the  $F_2$  generation, and his curves for the distribution of  $F_3$  progenies were very like those of Briggs. But Briggs postulated that there was a major factor for resistance allowing about half the heterozygous plants to become infected, while Churchward suggested that susceptibility was dominant and that low infections were caused by unfavorable enviroinal conditions. It seems possible that for both Briggs' and Churchward's hybrids there may have been a type of factor interaction similar to that demonstrated for the reaction of Feterita hybrids to the covered smut, and that the environment might determine the dominance of resistance or susceptibility and the hybrid ratios obtained.

Hybrids of Monarch  $\times$  Hull-less oats inoculated with the loose smut (to which Monarch is resistant and Hull-less susceptible), and of Gothland  $\times$  Hull-less inoculated with covered smut (to which Gothland is resistant and Hull-less susceptible) were reported by Reed (1932b), and show similar reactions.  $F_2$  plants of the first cross gave 31.3 per cent infection with the loose smut, and only a small proportion of  $F_3$  progenies were completely resistant. Agreement to a 1:2:1 ratio was close only if progenies giving up to 15 per cent were considered infected, and the distribution of  $F_3$  progenies was similar to that of Feterita hybrids under the 1932 environment.  $F_2$  plants of the second cross gave 46 per cent infection with the covered smut, and the distribution of  $F_3$  progenies is more suggestive of that for Feterita hybrids in 1934. The resistant parents brought into every one of these crosses all gave occasional smutted plants, another indication that the type of resistance possessed by these varieties and Feterita may be similar.

The epistatic relation of one factor to another has also been reported for several genetic studies of rust resistance. Investigating the reaction of oat hybrids to *Puccinia graminis Avenae*, Dietz (1928) found that a 13:3 ratio of susceptible to resistant  $F_2$  plants occurred in a cross between White Russian (resistant) and Burt (susceptible). He postulated that

a factor inhibiting resistance was brought into the cross by Burt. Segregation of  $F_3$  progenies showed a close agreement to a 1:2:6:7 ratio, confirming this hypothesis. However, data for other crosses were variable, resistance being dominant in some and recessive in others, with 3:1 and 13:3 ratios occurring. A similar type of factor interaction was noted by Dietz and Murphy (1930).

Reaction to stem rust of wheat was studied by Neatby and Goulden (1930) in crosses between H-44-24 (resistant) and Reward (susceptible).  $F_2$  ratios indicated a one factor difference with susceptibility dominant, but two distinct types of segregating  $F_3$  progenies occurred, some showing the dominance of resistance. It was postulated that there was a modifying factor inhibiting resistance brought in by the susceptible parent. Data for crosses between Reward and Hope showed a three factor segregation. The effect of the factor inhibiting resistance was only partial when one of these factors was homozygous and the other heterozygous, i.e., when the balance was altered in favor of resistance. Data for a cross between Webster and H-24-44 indicated that Webster brought in a factor for susceptibility which, when homozygous, was epistatic to the factor for resistance brought in by H-44-24.

Clark and Humphrey (1933) and Clark and Smith (1935) crossed Hope with susceptible varieties and could not agree with Neatby and Goulden that susceptibility was due to a dominant factor inhibiting the effect of the Hope factor. Clark and Humphrey postulated that resistance was dominant, Neatby and Goulden that susceptibility was dominant, but all agreed that either susceptibility or resistance was inhibited by a second factor.

Kulkarni (1934), studying the reaction to stem rust of a hybrid between Hope (resistant) and Liguleless (susceptible) found that a 3:13 ratio of resistant to susceptible plants occurred in the  $F_2$  generation and that the distribution of  $F_3$  progenies gave a close agreement to a 1:2:6:7 ratio, due, he believes, to a factor brought in by Liguleless having an inhibiting influence on a factor for resistance brought in by Hope.

All these authors agreed that their data indicated the interaction of factors opposite in reaction, in some cases a factor for resistance and in others a factor for susceptibility being the modifying one. Great variability in results has been reported throughout. That the environment partly accounted for this, has been suggested in some of these investigations outlined, but in none has it been postulated as the primary agent governing which of the two interacting factors should exercise a dominant effect. Feterita hybrids inoculated with the covered smut have shown the same type of factor interaction, and it has been demonstrated that a balance exists between these opposing factors, which external conditions alone

can throw one way or the other. Thus the environment determined the dominance of resistance or susceptibility and the hybrid ratios obtained.

Inheritance of this type is in striking contrast to that demonstrated in the reaction of Milo hybrids to the covered smut, and the simple Mendelian inheritance reported in numerous cases. In such hybrids the effect of the environment is of far less consequence. In these, it would seem that factors influencing reaction to disease all act in one direction, and that there is not the balanced antagonistic action of two opposing forces, which can be shifted one way or the other by very slight influences.

#### SUMMARY

Genetic studies on the resistance of sorghum hybrids to the loose and covered kernel smuts, *Sphacelotheca cruenta* and *Sphacelotheca Sorghi*, have been carried out.

Seeds were germinated under four different sets of enviroanal conditions and it was discovered that the susceptible varieties gave highest infections when germinated in sand with 10 per cent moisture, particularly when supplied as a 2 per cent sucrose solution. Dwarf Yellow Milo maintained its resistance under this favorable infection environment but, in respect to *Sph. Sorghi*, Feterita exhibited pathological effects of infection not noted before. This infection was characterized by a complete or partial blasting of the heads, with the production of occasional smut balls, and also by excessive tillering and branching.

The four susceptible varieties, Shallu, Dakota Amber Sorgo, Dawn Kafir, and Sumac Sorgo, and the two resistant varieties, Dwarf Yellow Milo and Feterita, were used as parents.

Crosses were made (1) between the resistant varieties, Dwarf Yellow Milo and Feterita, (2) between Dwarf Yellow Milo and susceptible varieties, and (3) between Feterita and susceptible varieties. Infection reactions with the covered smut indicated that when Dwarf Yellow Milo was crossed with Feterita approximately one-sixteenth of the  $F_2$  plants were susceptible, confirming the assumption that these varieties possessed different factors for resistance. When Dwarf Yellow Milo was crossed with susceptible varieties approximately one-fourth of the  $F_2$  plants were susceptible. It was suggested that Dwarf Yellow Milo brought into the crosses a factor for resistance (R) completely epistatic to a factor for susceptibility (S) brought in by the susceptible varieties.

When Feterita was crossed with susceptible varieties, the results indicated the interaction of the factor for susceptibility (S), and a factor for resistance brought in by Feterita (B). Under enviroanal conditions highly favorable for infection, S has been demonstrated to be epistatic to B, for

segregation in the  $F_2$  generation, as reconstructed from  $F_3$  data, approximated the ratio of 13 smutted to 3 normal plants. Under environmental conditions less favorable for infection,  $F_2$  ratios were nearly reversed, approaching the ratio of 3 resistant to 1 susceptible plant. On the basis of these data it has been concluded that hybrid plants containing both the S and B factors were extremely unstable in their infection reactions, and that the epistasis of S over B, or B over S, was determined solely by environmental conditions during the germination period.

Infection results with the loose smut indicated that when Dwarf Yellow Milo was crossed with susceptible varieties there was a two factor interaction similar to that of Feterita hybrids inoculated with the covered smut. When Feterita was crossed with susceptible varieties there was clear-cut dominance of resistance, and results indicated the interaction of three factors. No infected plants were obtained from crosses of Feterita with Dwarf Yellow Milo, indicating that these two varieties possessed at least one factor for resistance in common. It has been suggested that the factors governing reaction to *Sph. Sorghi* may also determine the reaction to *Sph. cruenta*, but that their effect is reversed. The presence of an additional factor influencing *Sph. cruenta* reactions has complicated the ratios, and additional data would be necessary for a more precise analysis of these results.

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BROOKLYN, N. Y.

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## The Ophioglossaceae of New Jersey,<sup>1</sup> a study in local distribution

R. T. CLAUSEN AND J. L. EDWARDS

(WITH PLATE 7 AND SEVEN TEXT-FIGURES)

From the available manuals and local floras, one can obtain only the vaguest sort of information concerning the detailed distribution of the *Ophioglossaceae* in New Jersey. When the writers began first to study the fern flora of their native state, this lack of distributional data, as well as the apparent confusion concerning the taxonomic status of a number of the forms within the selected area, attracted them to give particular attention to this group.

Taylor (1915), in the most recent attempt to write a flora of the New York region, lists one species of *Ophioglossum* and seven of *Botrychium* from New Jersey. In his flora, the statements concerning distribution are quite unsatisfactory and give one the impression that certain of the species are decidedly rare, when this is not at all the case. The information concerning distribution given by Small (1935) in his *Ferns of the Vicinity of New York* is too general to be very helpful in clarifying the situation in New Jersey.

In 1922, Long discussed very fully and carefully the distribution of *Botrychium matricariaefolium* in New Jersey. Although his paper represents the results of all the data that was then available, one would probably not conclude from it that the species discussed is actually common and wide-ranging throughout the northern part of the state.

The present paper is offered in an attempt to bring up to date our knowledge of the distribution of *Ophioglossum* and the species of *Botrychium* in New Jersey in the light of intensive collecting and exploration during the last few years. The taxonomic concepts and nomenclature here employed are those adopted by the senior author in his as yet unpublished *Monograph of the Ophioglossaceae*. Briefly, species have been considered to represent the smallest natural populations not definitely connected by an intergrading series in the line of biotypes. Subspecies are interpreted as the broader divisions of species, usually with a definite geographical range and distinguished from one another by generally more than one character; while those minor variations of species, based on such trivial characters as leaf cutting, pubescence and habit, without regard to range, are considered as varieties. It is realized that these criteria are somewhat different from

<sup>1</sup> The maps in this paper are used through the courtesy of the McKinley Publishing Company, Philadelphia, Pa.

those accepted by certain other students of taxonomy, but this is not the place for an exposition of these details. A full discussion of this matter will be presented elsewhere by the senior author.

No attempt will be made here to give a complete synonymy for each species, but only those names used in the more important recent papers and manuals will be listed and these only when they are different from the ones adopted by the writers. The key is adapted from the senior author's (1934) unpublished *Studies in the Genus Botrychium in Northeastern North America*, of which a few typewritten copies have been available since 1934. Portions of this key have been used, without acknowledgment, in a recent work on ferns.

Names of herbaria have been abbreviated as follows:

B—Brooklyn Botanic Garden Herbarium

Claus—Private herbarium of R. T. Clausen

Edw—Private herbarium of J. L. Edwards

G—Gray Herbarium

Gris—Private herbarium of L. Griscom

M—Herbarium of the Missouri Botanical Garden

Ph—Herbarium of the Philadelphia Academy of Natural Sciences

Princ—Princeton University Herbarium

Rut—Rutgers University Herbarium

U—United States National Herbarium

Y—New York Botanical Garden Herbarium

#### KEY TO THE OPHIOGLOSSACEAE OF NEW JERSEY

1. Sterile blade variously lobed or divided, rarely simple; venation open; sporangia separate, in simple or compound spikes. . . . . *Botrychium*—2
2. Blades various, but not at once lax and membranous, broadly deltoid and sessile. Bud completely enclosed by the sheathing base of the stalk. Bud hairy or smooth. . . . . 3
3. Bud hairy; sterile blade ternately decompound, rather long stalked, inserted near the base of the plant. . . . . Subgenus *Sceptridium*—4
4. Segments of blade all of about same size and shape, ovate or obovate, the chief terminal divisions not elongate. Blade usually somewhat fleshy, light green. Spores maturing in August or September, a month earlier than the following species. . . . .  
     . . . . . *B. multifidum*, subsp. *silatfolium*
4. Segments of blade not all of same size, the chief terminal divisions usually elongate, little divided. Blade either not fleshy or less so than the above. Spores maturing in September and October. . . . . *B. dissectum*—5
5. Segments of blade not deeply and finely toothed or divided. . . . . 6
6. Ultimate divisions of blade obtuse or rounded. . . . . *B. dissectum*, var. *oneidense*
6. Ultimate divisions of blade acute or acutish. . . . . *B. dissectum*, var. *obliquum*
5. Segments of blade deeply and finely toothed or divided. . . . .  
     . . . . . *B. dissectum*, var. *typicum*
3. Bud smooth; sterile blade usually small and pinnately divided, rarely simple, sessile or short-stalked, parting from the common stalk at various heights. . . . .  
     . . . . . Subgenus *Eubotrychium*—7

7. Fertile spike erect in the bud, with the sterile blade erect or slightly inclined over it. Segments of sterile blade usually obovate. Spores large, 33–52 $\mu$  in diameter..... *B. simplex*—8
8. Sterile blade extremely slender, inserted towards the summit of the plant. Plants of swamps and wet woods..... *B. simplex*, var. *tenebrosus*
8. Sterile blade inserted towards the middle of the plant. Plants of dry woodlands..... *B. simplex*, var. *laxifolium*
7. Fertile spike and sterile blade wholly or partially bent down in the bud. Segments of the blade oblong and obtuse or lanceolate and acute. Spores rather small, 24–48 $\mu$  in diameter..... 9
  9. Apex of fertile spike bent down in the bud, with the apex of the sterile blade bent down over and covering it. Sterile blade usually, but not always, stalked, inserted towards the summit of the plant; the divisions obtuse..... *B. matricariaefolium*
  9. Fertile spike and sterile blade both entirely bent down in the bud, with the fertile spike recurved its whole length, and the shorter sterile blade reclined upon it. Sterile blade sessile, inserted at the summit of the plant; the divisions narrow (1–2.5 mm. wide) and acutish..... *B. lanceolatum*, subsp. *angustisegmentum*
2. Sterile blade sessile, large, deltoid, much divided, thin in texture. Bud partially exposed by the sheathing base of the stalk, which is open on one side. Bud hairy..... Subgenus *Osmundopteris*  
..... *B. virginianum*
1. Sterile blade simple; venation netted; sporangia coherent in a simple spike..... *Ophioglossum vulgatum*

***Botrychium multifidum* (Gmel.) Rupr., subsp. *silaifolium* (Presl) Claus., comb. nov.**

*B. silaifolium* Presl, Rel. Haenk. 1: 76. 1825.

*B. ternatum*, var. *australe* (in part) and subvar. *intermedium* D. C. Eaton, Ferns of North America 1: 149. 1879.

*B. ternatum* (Thunb.) Sw., var. *intermedium* D. C. Eaton of Gray's Manual, ed. 7. p. 49. 1908.

*B. multifidum* (Gmel.) Rupr., var. *intermedium* (D. C. E.) O. A. Farwell, Rep. Mich. Acad. Sci. 18: 87. 1916.

This, the most widespread form of the subgenus *Sceptridium* in North America, has probably experienced more nomenclatorial changes than any other of our species. As considered here, the American subspecies, which occurs in New Jersey, represents a well-marked geographical race of the circumpolar *B. multifidum*. The Old World form of the species, which has never been found in New Jersey, is *B. multifidum typicum*. It was described originally from Russia in 1768 and is the small plant that is found throughout northern Europe and Asia and that has been treated in the manuals as *Matricariae* and *rutaefolium*. This typically Old World race reaches northeastern North America in Newfoundland, eastern Canada, northern New England and New York, where it passes insensibly into the

larger, more lax subspecies *silaiifolium*. In Siberia, the typical element passes into the subsp. *robustum* (Rupr.) Claus.,<sup>2</sup> which seems to be the dominant form in Alaska. To the south this subspecies passes into *silaiifolium*. Since it has not been possible to separate the eastern American plants from those occurring in Washington and British Columbia, it has seemed best to treat them together as one subspecies, extending from Quebec and Maine to northern New Jersey and west to Washington, Oregon and British Columbia.

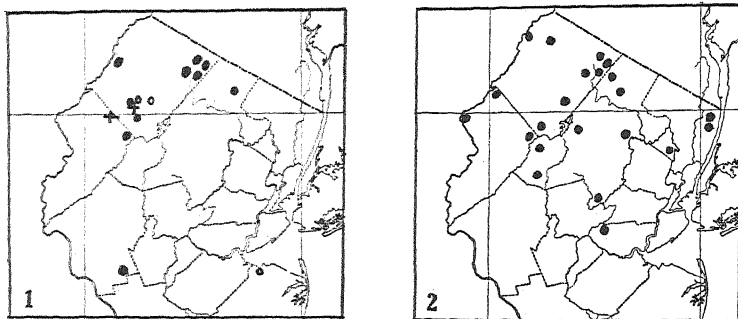


Fig. 1. New Jersey range of *Botrychium simplex*, var. *tenebrosum* (dots), var. *laxifolium* (crosses) and *B. multifidum*, subsp. *silaiifolium* (circles).

Fig. 2. New Jersey range of *Botrychium lanceolatum*, subsp. *angustisegmentum*.

Although Small (1935) lists *B. multifidum* for the New York region, it is quite evident from his text that he is discussing *B. silaiifolium* of Presl and not Gmelin's species, which is synonymous with *B. matricariae*.

In New Jersey, this is one of our rarest forms, known definitely only from three stations in Sussex County, where it grows in rather dry deciduous woodlands, from one in Morris County and from one place in Monmouth County. Monmouth: Keyport, *M. Carhart* (Y). Morris: Lake Hopatcong, *T. C. Porter* (Princ). Sussex: Andover, *J. L. E.* and *R. T. C. 128* (Claus); Sparta, *J. L. E.* (Edw); and Newton, *M. Carhart* (Y).

The Keyport specimen consists of a single, membranous, sterile blade, not yet fully developed. Although this plant is not entirely typical, it does not seem possible to refer it to any other species. The occurrence on the coastal plain of a strictly northern form is not unusual or unparalleled. For example, at Browntown, also in Monmouth Co., *Nemopanthis mucro-*

<sup>2</sup> *Botrychium multifidum* (Gmel.) Rupr., subsp. *robustum* (Rupr.) Claus., comb. nov.

*B. rutaefolium* A. Br., var. *robustum* Rupr. in Milde, Nova Acta 26: 763. t. 55 f. 9. 1858.

*B. robustum* (Rupr.) Und., Bull. Torr. Club 30: 51. 1903.

*nata*, which is characteristically a plant of the northwestern part of the state, is found in some of the bogs. Other similar cases might be mentioned.

*BOTRYCHIUM DISSECTUM* Sprengel, var. *ONEIDENSE* (Gilbert) Farwell, Papers Mich. Acad. Sci. 3: 89. 1924.

*B. ternatum*, var. *oneidense* Gilbert, Fern Bull. 9: 27. 1901.

*B. dissectum* Sprengel, f. *oneidense* (Gilbert) Clute, Fern Bull. 10: 76. 1902.

*B. obliquum* Muhl., var. *oneidense* (Gilbert) Waters, Ferns, p. 334. 1903.

*B. multifidum* (Gmel.) Rupr., var. *oneidense* (Gilbert) Farwell, Rep. Mich. Acad. of Science. 18: 86. 1916.

This is one of the most distinct leaf forms of the *B. dissectum* group. The thin texture of the foliage blade, the elongate penultimate segments, the late fruiting time and the regular association with the other forms of *B. dissectum* indicate that it should rightfully be treated as a variety of that species and not of *B. multifidum* as has been done by several recent authors (Farwell, 1916 and Graves, 1935). It is true that this variety suggests *B. multifidum*, subsp. *silaifolium* in the blunt divisions of the blade and in retaining the green leaf color throughout the winter, but it seems always to be readily separated from that species by the other characters mentioned above. Although no true intergradation between the two species has been observed, it is felt that var. *oneidense* represents that form of *B. dissectum* which comes nearest to *B. multifidum*. Careful study of the retention of the green color of the blades throughout the winter indicates that although the majority of the plants of *B. dissectum*, vars. *typicum* and *obliquum* turn to bronze in the late autumn, a rather considerable number of them remain quite green, hence too much significance should not be attached to this character.

In New Jersey this is a plant of moist woodlands, where it grows in association with *B. dissectum*, var. *obliquum*. The following sheets may be cited as typical. Bergen: Cresskill, *H. Dautun* (B). Sussex: Cranberry Lake, *K. K. Mackenzie* 2455 (Y). Somerset: Bound Brook, *H. M. Denslow* (Y). In the Princeton Herbarium is a specimen from Cooper's Creek near Camden. We also have a doubtful specimen from Twin Bridges, near Lincoln Park, Morris County.

*BOTRYCHIUM DISSECTUM* Sprengel, var. *OBLIQUUM* (Muhl.) Clute, Fern Bull. 10: 76. 1902.

*B. obliquum* Muhl. in Willd. Sp. Pl. 5: 63. 1810.

*B. dissectum* Sprengel, f. *obliquum* (Muhl.) Fernald, Rhodora 23: 151. 1921.

In New Jersey, this, our second commonest kind of Grape-fern occurs in a variety of habitats, including rich swampy woods, dry woodlands, thick-



ets and rarely sandy banks in the pine barrens. Widely distributed throughout the state, the var. *obliquum* is least common in the pine barren area. In the herbaria examined no specimens were seen from Hudson and Somerset Counties, although the plant undoubtedly occurs in all counties of the state. The collection (Ph) of E. T. Wherry from Far Hills, Somerset Co., on Aug. 28, 1935 seems to be var. *oneidense*.

The following typical specimens from the various counties may be cited. Atlantic: Hammonton, *F. L. Bassett* (G). Bergen: Closter, *C. F. Austin* (Y). Burlington: Kinkora, *B. Long*, 10974 (Ph). Camden: Camden, *C. F. Parker* (M). Cape May: Ocean View, *B. Long* 25042 (Ph). Cumberland: Hoffmans' Mill, *J. M. Fogg, Jr.* 5977 (Ph). Essex: Caldwell, *H. M. Denslow* (Y). Gloucester: Mullica Hill, *B. Long* 14274 (Ph). Hunterdon: Bowne's Station, ex herb. *H. L. Fischer* (Ph). Mercer: Princeton, *J. E. Peters* (Rut). Middlesex: Spotswood, *M. A. Chrysler* (Ph, Rut). Monmouth: Eatontown, *A. T. Beals*, *G. W. Bassett* & *A. J. Slayter* 9428 (Ph). Morris: Twin Bridges, *R. T. Clausen* 119 (Claus). Ocean: Bamber, *J. L. E.* & *R. T. C.* 1089 (Claus). Passaic: Allwood, *R. T. C.* 117 (Claus). Salem: Riddleton, *J. M. Fogg, Jr.* 6145 (Herb, U. of Penn., Rut). Sussex: Stockholm, *W. M. Van Sickle* (U). Union: New Providence, *W. H. Leggett* (Rut). Warren: Blairstown, *E. T. Wherry* (Ph).

The var. *pennsylvanicum* described by Graves (1935) and represented by a number of New Jersey specimens seems unworthy of nomenclatorial distinction. If we were to recognize this trivial form, we would then be obliged to describe about fifty other similar variations in order to be consistent.

#### BOTRYCHIUM DISSECTUM Sprengel, var. TYPICUM

*B. dissectum* Sprengel, *Anleit.* 3: 172. 1804.

*B. obliquum* Muhl., var. *dissectum* (Spreng.) Prantl, *Jahrb. Bot. Gart. Berlin.* 3: 342. 1884.

It is most regrettable that this, the atypical form of a widely distributed and variable species, should stand as the nomenclatorial type for the species, but if we are to abide by the International Rules of Nomenclature which state that the first validly published name to be applied to any part of a species must be considered as the proper name for that species, no other alternative is possible. To us it seems more likely that the wide ranging *B. obliquum* of Muhlenberg represents the morphological type of the species. Variation has taken place from this type in various directions. *B. dissectum* Spreng. represents the dissected leaf condition, while *oneidense* seems to represent a prolongation of the juvenile, blunt lobed condition of the blade. Very young sporophytes of the forms of the *B. dissectum* com-

plex look much alike. All have the divisions blunt and finely serrate, but extreme forms of the dissected variety show the laciniate character at an early age. As the plants become older, vars. *obliquum* and *typicum* develop their distinctive characters, but var. *oneidense*, although it develops in size, retains the juvenile, rounded segments of the blade.

As may be seen from the accompanying map (map 4), the var. *typicum* is not as common in New Jersey as the var. *obliquum*, although it has approximately the same range and habitat preferences. Usually the two varieties grow together in colonies, but they are almost always distinct and show little evidence of intergradation such as is found in the fields and pastures of central New York and New England.

Atlantic: Mays Landing, *W. Stone 13261* (Ph). Bergen: Closter, *C. F. Austin* (U, Y). Burlington: Crowleystown, *B. Long 18332* (Ph). Camden: Somerdale, *B. Long 22518* (Ph). Cape May: Cape May, *E. P. Killip* (U). Essex: Montclair, *F. H. Blodgett* (Y). Gloucester: Mantua, *B. Long 22648* (Ph). Hudson: Hoboken, *ex Torrey herb.* (Y). Mercer: Princeton, *J. E. Peters* (Prnc). Middlesex: New Brunswick, *F. H. Blodgett* (Y). Monmouth: Keyport, *B. Long 20867* (Ph). Morris: Mt. Tabor Pond, *G. W. Bassett* (Ph). Ocean: Manahawken, *B. Long 13485* (Ph). Passaic: Allwood, *R. T. C. 108* (Claus). Salem: Sharptown, *B. Long 14106* (Ph). Somerset: Bernardsville, *W. D. Miller 1697* (Y). Sussex: Brickhouse, *J. L. E. & R. T. C. 107* (Claus). Union: New Providence, — (Y). No specimens have been seen from Cumberland, Hunterdon, or Warren counties.

**Botrychium simplex** Hitchcock, var. **tenebrosum** (A. A. Eaton) Claus., comb. nov.

*B. tenebrosum* A. A. Eaton, Fern Bull. 7: 8. 1899.

Although this diminutive moonwort is by no means uncommon in northwestern New Jersey, yet it is not recorded from the state by Taylor (1915) and merely passing notice is given it by Small (1935). Many recent authors have merged *tenebrosum* with *B. simplex*, not considering it worthy of any nomenclatorial recognition. Actually, on a basis of our experience in northern New Jersey, we should say that *B. tenebrosum* forms a very distinct population, quite constant in its characters and not intergrading with any other form. Only after we had surveyed large series of herbarium specimens from northern New England, New York, and southern Canada, which clearly demonstrated a complete intergradation between this and typical *simplex*, were we convinced that *tenebrosum* could not be maintained as a species. Since this slender variety occurs at various places throughout the range of the *B. simplex* complex, it has not been possible

to consider it as a geographical race. Consequently it is here treated as a variety of *simplex*. The var. *angustum* Milde resembles our variety in some respects, but is not considered by us to be the same as var. *tenebrosum*.

We might recharacterize this variety as: plants glabrous, very slender, 1–25 cm. high; base of stalk enclosing bud, covered by brown sheathing bases of preceding years' stalks; fertile segment erect in the bud, sterile segment usually with the apex slightly inclined over (but not covering) tip of fertile spike; sterile blade not sessile, inserted above the middle, usually towards the summit of the plant; blade simple or lobed, in old plants with two or three pairs of subopposite, obovate-oblong lobes; fertile spike simple or once pinnate; spores finely vermiculated or verrucose, large, 38–52 $\mu$  long (averaging about 42 $\mu$ ).

Gametophytes with young sporophytes attached have been found in low wet woods at Springdale and at Mud Pond, both in Sussex County. These are small flattened brownish bodies, 3–4 mm. long and about 1.5 mm. wide. The roots are developed from the dorsal surface, to the side of the prothallium, while the stem apex differentiates from the center where the roots originate and grows upward from this point. Thus, the sporophyte is developed entirely on the upper surface of the gametophyte, which probably remains attached to the young plant for several years, before it has disappeared completely through decay. Sporophytes with gametophytes attached ranged from very minute to quite large. At Mud Pond, the largest specimen obtained with a good, undecayed gametophyte attached, was 17 cm. high, with a pinnately divided spike 3.3 cm. long, of which the sporangia were shedding abundant spores! The foliage blade in this specimen was as well developed as is ever the case in this variety.

The var. *tenebrosum* is found in our region in damp, heavily shaded woods and at the edges of deep swamps. At the Springdale station, which was apparently first discovered by H. W. Pretz in 1907, the plants grow in considerable abundance in slightly acid soil on rich, swampy bottom land and in the *Thuidium* moss on hummocks and on old decaying logs. *Ophioglossum vulgatum* grows here in the same restricted area. The trees and shrubs shading the little ferns are mostly elms, hickories and spice-bushes, while associated on the same hummocks with the *Botrychium* are *Osmunda regalis* and *Liparis Loeselii*. At Mud Pond the plants grow in the moss in moist rich woods under *Acer saccharum*, in association with *B. lanceolatum*, subsp. *angustisegmentum* and *B. matricariaefolium*. At most of the other stations which will be cited, the habitat is similar.

Passaic: Midvale, J. L. E. (Edw); also A. N. Leeds 3645 in part (Ph); Upper Macopin, J. L. E. (Edw). Sussex: Springdale, J. L. E. & R. T. C. 85 (Claus, Edw); also H. W. Pretz 497 (Ph); Mud Pond, Stockholm, J. L. E.

& *R. T. C. 1210* (Claus, Edw); Cherry Valley, between Wawayanda Lake and Moe, *J. L. E. & R. T. C. 1211* (Claus); Canistear Reservoir, *J. L. E.* (Edw); Breakneck Mt., Vernon, *J. L. E.* (Edw); Wallpack Center, *Britton and Rusby* (Rut). Warren: Allamuchy, *J. L. E. & R. T. C. 1209* (Claus).

***Botrychium simplex*** Hitchcock, var. ***laxifolium*** Claus., var. nov.

Planta laxa lamina membranacea et inserta ad medium; segmentis laminae obovatis et fere remotis.

Plant lax with the blade membranous and inserted medianly; the divisions of the blade obovate and rather remote.—Dry woodlands of Vermont, Massachusetts, Connecticut, New York and New Jersey. Type in Clausen Herbarium, from dry shady woods over limestone rocks, Johnsonburg, Warren Co., N. J., June 24, 1933, *J. L. Edwards* and *R. T. Clausen*, no. 80.

In New Jersey this variety is known only from Johnsonburg, Warren County, in the heart of a limestone region. It was apparently first discovered near there at Glover Pond on June 11, 1921, by L. Griscom and K. K. Mackenzie 10602 (Gris, Y); then in May, 1933, the senior author found it in dry woods on a slope by the Lackawanna Railroad cut. We visited that place in June of that year and collected specimens. There were about fifty plants in the colony, which represented the extremes in leaf form as shown in the plate (pl. 7). Samples of the soil from about the bases of the plants gave a slightly acid reaction. Associated species were *Rhus typhina*, *Viburnum acerifolium*, *Betula lenta*, *Acer saccharum*, *Collinsonia*, *Cornus*, and *Similacina*.

The spores of the Johnsonburg plants average about  $42\mu$  in diameter. The markings of the spore coats vary considerably, even in spores from the same plant. The general pattern may be described as an irregular network, appearing almost as small points on the germinating surface. The buds of these plants are slender, with both the fertile and sterile segments erect, but in one or two cases there is a slight inclination of the apex of the sterile portion over the top of the fertile spike.

Since Milde's many described varieties of *B. simplex* seem to represent mere age forms of the same thing, it has seemed desirable to give the present variation a new name, rather than to try to alter the concept of one of Milde's varieties to include our plants. A few specimens from various parts of the range of this variety are cited here. VT. Addison: Middlebury, *E. Brainerd* in part (G, Ph, Y); Bennington: Manchester, *M. A. Day* 246 (G). MASS. Berkshire: Pittsfield, *G. G. Kennedy* (G). CONN. Windham: Woodstock, *C. A. Weatherby* and *A. W. Upham* (G), this not

entirely typical, but approaching the variety. N. Y. Saratoga: West Charlton, *H. K. Svenson* (B).

No specimens have been seen to support reports of *B. simplex* from Andover Junction or Plainfield in New Jersey.

*BOTRYCHIUM MATRICARIAEFOLIUM* Al. Braun in Döll, Rheinische Flora. p. 24. 1843.

Not *Osmunda ramosa* Roth, Flor. Germ. 2: 444. 1788.

*B. ramosum* Ascherson, Flor. Prov. Brandenburg. p. 906. 1864.

*B. neglectum* Wood, Classbook of Botany. p. 635. 1847.

In 1788, A. W. Roth described *Osmunda ramosa* as a new species. This was based on material which later students have shown to be a peculiar form of *B. Lunaria*, and therefore the name *ramosum* should not be applied to the plant which we now designate as *matricariaefolium*. The American form of the species, described by Wood as *B. neglectum*, is not considered sufficiently different from the Old World form to warrant even sub-specific recognition.

Although *B. matricariaefolium* is reported from only two stations in New Jersey by Taylor (1915) and is said by Small (1935) "to be confined mainly to the more northern provinces, where it occurs at 4000 feet altitude," we know this to be the commonest and most widely distributed member of the subgenus *Eubotrychium* in our area, found at elevations from 100 to 1400 feet. As Long (1922) suggested would be the case, a greater frequency is now known in the northern counties than former collections indicated.

Just as the range of variation in the cutting of the sterile blade is extreme, so this species seems to be able to survive in a variety of habitats. We have found it growing in dry sandy woods, rich swamps, rocky woods and in sandy thickets. In central New York, the senior author has found it abundant in dry sterile fields, where the plants assume a leathery, compact character.

In the citation of recent specimens, only those old collections are included which were not mentioned by Long. Bergen: Closter, *C. F. Austin* (Ph). Burlington: Marlton, *H. E. Stone* (Ph). Gloucester: Mickleton, *B. Long 27748* (Ph); Mullica Hill, *B. Long 27293* (Ph). Middlesex: South

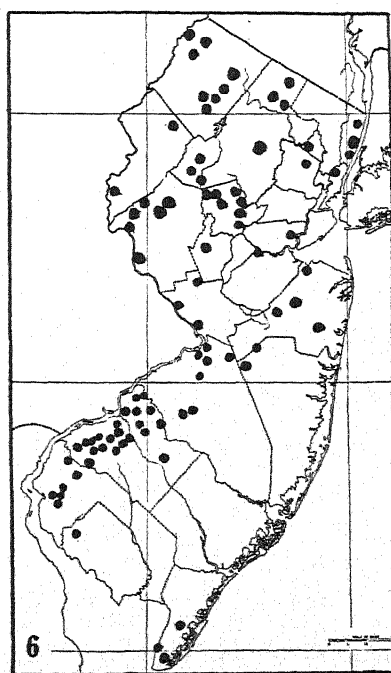
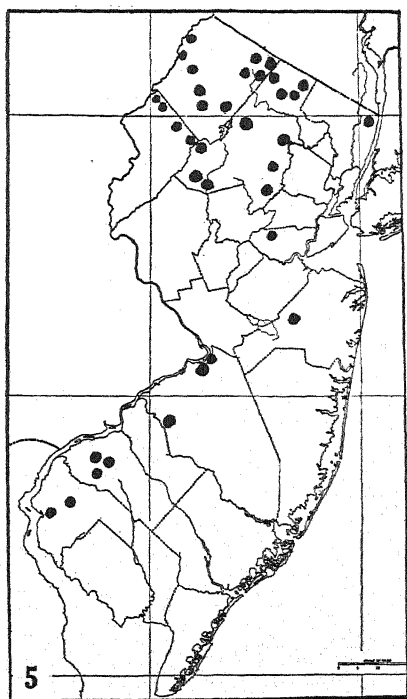
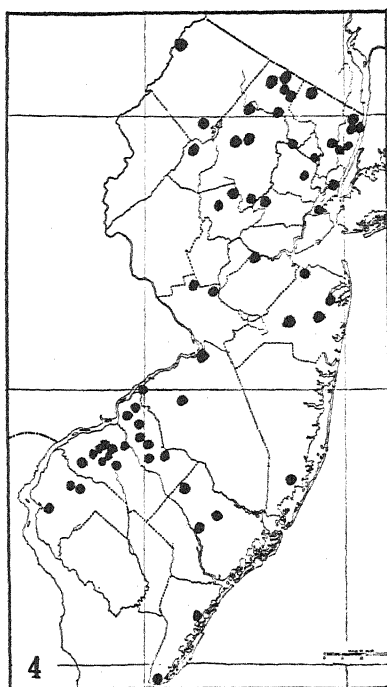
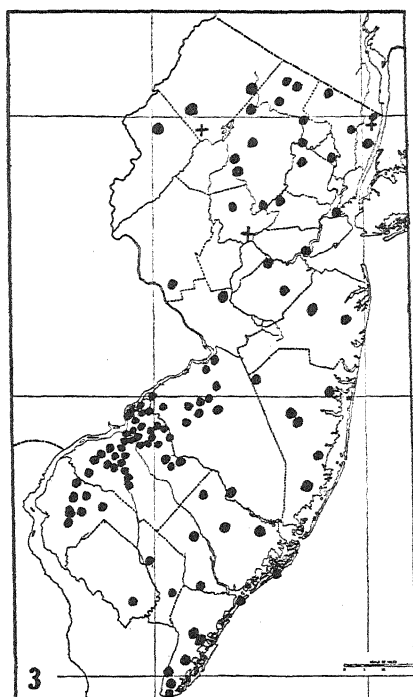
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Fig. 3. New Jersey range of *Botrychium dissectum*, var. *oneidense* (crosses) and var. *obliquum* (dots).

Fig. 4. New Jersey range of *Botrychium dissectum*, var. *typicum*.

Fig. 5. New Jersey range of *Botrychium matricariaefolium*.

Fig. 6. New Jersey range of *Botrychium virginianum*.



Plainfield, *W. D. Miller 1695* (Y). Morris: Budd's Lake, *L. Bowen, W. Highton, W. Rusling, J. L. E. & R. T. C. 1717* (Claus); Long Valley, *E. T. Wherry* (Ph); Littleton, *J. L. E.* (Edw); Towaco, *J. L. E.* (Edw); Big Swamp, — (Rut). Passaic; Midvale, *A. N. Leeds 3645* in part (Ph); Upper Macopin, *J. L. E.* (Edw); Ringwood Junction, *K. K. Mackenzie* (Y); Uttertown, *J. L. E.* (Edw). Salem: Salem, *S. Johnson* (G, Ph). Sussex: Springdale, *J. L. E. & R. T. C. 94* (Claus); Sparta, *J. L. E. & R. T. C. 102* (Claus, Edw); Canistear Reservoir, *J. L. E.* (Edw); Mud Pond, *J. L. E. & R. T. C. 1206 & 1207* (Claus, Edw); Breakneck Mt., Vernon, *J. L. E.* (Edw); Wallpack Center, *J. L. E.* (Edw); Montague, *J. L. E. & R. T. C. 97* (Claus, Edw). Warren: Allamuchy, *E. T. Wherry* (Ph); also *J. L. E.* (Rut); Glover Pond, Johnsonburg, *J. L. E. & R. T. C. 103* (Claus); Hardwick, *J. L. E.* (Edw); Millbrook, *J. L. E.* (Edw).

In the field notes of the late W. D. Miller, under date of May 31, 1926, there is a note concerning a colony of plants of this species in a clearing in woods by a deserted house at the Lahaway Plantations in Ocean County. Search for specimens to substantiate this report has been unsuccessful, but there is no reason to doubt the occurrence of this species there in the pine barrens, since it was reported by Long from Clementon, in Camden Co., where it grows in "dry, open sandy thickets on the borders of pine woods."

***Botrychium lanceolatum* (Gmel.) Angstr., subsp. *angustisegmentum***  
(Pease and Moore) Claus., comb. nov.

*B. lanceolatum* (Gmel.) Angström, var. *angustisegmentum* Pease and Moore. *Rhodora* 8: 229. 1906.

*B. angustisegmentum* (Pease and Moore) Fernald. *Rhodora* 17: 87. 1915.

We have been unable to follow Prof. Fernald in considering the more lax, woodland plant of our northeastern states as representing a species distinct from the boreal typical *B. lanceolatum*. All of the characters used to separate *angustisegmentum* from *lanceolatum* fall down on close examination. The cutting of the sterile blade and the general appearance of the plants seem to be the best criteria for determining specimens as the one form or the other. Difference in spore size was given as one of the characters on which the segregation of *angustisegmentum* was based, but measurements of spores made by the senior author do not correspond with those furnished by Prof. Fernald (1915) in his paper on the species. He stated that the spores of *B. angustisegmentum* measured from 21–28 $\mu$  in diameter, while those of *B. lanceolatum* were from 35–45 $\mu$ . These measurements are considerably farther apart than the senior author's investigations would

indicate. Our data shows that the spores of the two forms overlap pretty much in size, although the extremes of typical *lanceolatum* are slightly larger than those of *angustisegmentum* and the averages show the spores of the boreal plant to be about  $5\mu$  larger than those of the more southern form. According to these measurements, *B. lanceolatum*, subsp. *typicum* has spores  $29-42\mu$  in diameter, av.  $35\mu$ ; while *B. lanceolatum*, subsp. *angustisegmentum* has spores  $24-37\mu$ , av.  $30\mu$ .

The size of the sporangia and the manner in which they are immersed in the sides of the branches of the fertile segment have not seemed constant enough characters for specific segregation, while the nature of the blade, with its narrower, thinner segments seems to be a definite response to the habitat in rich, shaded woods. Further, a number of specimens from southern Canada and western United States have seemed somewhat intermediate between the two forms. In the light of all of this evidence, we feel that *angustisegmentum* is best treated as a very distinct geographical race or subspecies of *B. lanceolatum*.

In New Jersey, the subsp. *angustisegmentum* is typically a plant of moist situations, around the edges of swamps and along streams, although it is occasionally found in dry beech and maple woods. It is confined to the middle and northern part of the state.

Bergen: Closter, *C. F. Austin* (Ph, Princ, U, Y); also *J. L. E. & R. T. C.* (Claus); Creskill, *H. Dautun* (B). Middlesex: South Plainfield, *J. L. E.* (Edw). Morris: Hook Mt., Towaco, *J. L. E.* (Edw); Long Valley, *E. T. Wherry* (Ph); Budd's Lake, *L. Bowen, W. Highton, W. Rusling, J. L. E. & R. T. C. 1716* (Claus); Berkshire Valley, *N. L. Britton* (Rut). Passaic: Passaic, *E. G. Knight* (Y); Upper Macopin, *J. L. E.* (Edw); Utertown, *J. L. E.* (Edw); west of Bearfort Mt., *W. D. Miller 1696* (Y). Sussex: Cranberry Lake, *H. W. Pretz 3653* (Ph); Sparta, *J. L. E.* (Edw); Canistear Reservoir, *J. L. E.* (Edw); Mud Pond, *J. L. E. & R. T. C. 1204* (Claus, Edw); Cherry Valley, between Wawayanda Lake and Moe, *J. L. E. & R. T. C. 1205* (Claus, Edw); Breakneck Mt., Vernon, *J. L. E.* (Edw); Lake Mashipacong, *K. K. Mackenzie* (Y); Montague, *J. L. E. & R. T. C. 90* (Claus, Edw). Warren: Allamuchy, *E. T. Wherry* (Ph); also *J. L. E.* (Rut); Dunnfield, *J. L. E.* (Edw); Flatbrookville, *E. B. Bartram* (Ph).

*BOTRYCHIUM VIRGINIANUM* (L.) Swartz, Schrad. Journ. Bot. 2: 111. 1800.

*Osmunda virginiana* L. Sp. Pl. 1064. 1753.

Our commonest species of *Botrychium*, the Rattlesnake Fern is found in woodlands throughout the state except in the pine barrens and in the coastal area just east of them, where it has apparently never been col-



lected. We have seen material from all counties except Atlantic and Union.

All of the New Jersey material belongs to the subsp. *typicum*, which is characterized by the large, lax, membranous, foliage blade with the pinnae divided to the midrib. The sporangia are brown, .6-.9 mm. in diameter, with the valves often recurved in dehiscence.

Bergen: Closter, *P. Wilson* (Y). Burlington: Vincentown, *B. Long* 11773 (Ph). Camden: Somerdale, *B. Long* 24017 (Ph). Cape May: Wildwood Junction, *B. Long* 21692 (Ph). Cumberland: Shiloh, *J. W. Adams* 876 (Herb. Univ. of Penn.). Essex: Montclair, *L. M. Stabler* (G). Gloucester: Swedesboro, *B. Long* 16105 (Ph). Hudson: Snake Hill, — (Y). Hunterdon: Ludlow, *W. M. Benner* 6435 (Ph). Mercer: Washington Crossing, *B. Long* 30472 (Ph). Middlesex: Woodbridge, *L. H. Lighthipe* (Y). Monmouth: Farmingdale, *B. Long & S. Brown* 3540 (Ph). Morris: Mt. Tabor, *K. K. Mackenzie* 2642 (M, Y). Ocean: New Egypt, *J. K. Grove* (Ph). Passaic: Haskell, Pompton, *H. M. Denslow* (Y). Salem: Auburn, *B. Long* 30798 (Ph). Somerset: Peapack, *R. C. Perry* (M). Sussex: Mud Pond, *J. L. E. & R. T. C.* 1213 (Claus). Warren: Johnsonburg, *J. L. E. & R. T. C.* 1212 (Claus).

OPHIOGLOSSUM VULGATUM L. Sp. Pl. 1062. 1753.

The Adder's-Tongue Fern is undoubtedly more common and more widely distributed than our records would seem to indicate, since it is so easily overlooked. In our area it is mostly a plant of damp meadows and of rich, wet woods, but in the southern part of the state it occurs in dry, sandy soil in open woods along the coast. This coastal material has been described by Mrs. Britton as *O. arenarium*, but these plants are not unlike slender or depauperate individuals which we have seen in otherwise normal colonies farther north. To us it seems best not to accord any nomenclatorial distinction to this purely ecological population.

Atlantic: Longport, *J. Crawford* (G, Ph, Y). Bergen: Closter, *C. F. Austin* (B, G. Ph, Princ, Y); Arcola, *J. L. E.* (Edw). Burlington: Medford, *S. Brown* (Ph); Browns Mills, *E. T. Wherry* (Ph); Marlton, *B. Long*

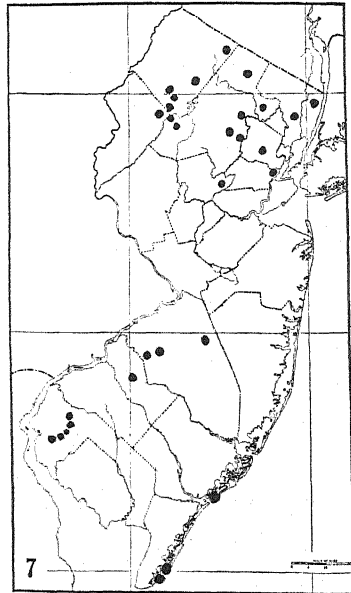


Fig. 7. New Jersey range of *Ophioglossum vulgatum*.

30660 (Ph). Camden: Lindenwold, *B. Long* 16293 (Ph). Cape May: Wildwood, *J. D. Crawford* and *C. L. Pollard* 3307 (B, G); Wildwood Beach, *C. S. Williamson* (Ph); Holly Beach, *E. G. Britton* (Y). Essex: West Orange, *R. C. Benedict* (Y). Gloucester: Clements, *B. Long*, 29767 (Ph). Morris: Hanover, *E. J. Pond* (U); Lee Meadows near Littleton, *J. L. E. & R. T. C.* 78 (Claus); Waterloo, *T. C. Porter* (Ph); Budd's Lake, *T. C. Porter* (Ph, Princ). Ocean: Beach Haven, *C. S. Williamson* (Ph). Passaic: Wolf Den Mt., *J. L. E.* (Edw); Stonetown, *J. L. E.* (Edw); Packanack Mt., *J. L. E.* (Edw). Sussex: Cranberry Lake, *H. W. Pretz* 2010 (Ph, Y); Springdale, *J. L. E. & R. T. C.* 172 (Claus); Sparta, *E. T. Wherry* (Ph); east side of Wawayanda Mt., *H. W. Pretz* 3622 (Ph). Salem: Fenwick, *C. D. Lippincott* (Ph); Mowers Station, *C. D. Lippincott* 132 (Ph); Penton, *B. Long* 23855 & 26288 (Ph); Riddleton, *J. Crawford* (Ph); also *B. Long* 14537 (Ph); Woodstown, *C. D. Lippincott* (Ph). Somerset: in little valley between First and Second Watchung Ridges, *M. A. Johnson* (Rut). Union: Great Island, Elizabethport, *A. M. Vail* (Y). Warren: Allamuchy, *J. L. Edwards* (Rut).

Although *O. vulgatum* is reported in the literature from Monmouth Co., we have seen no specimens from there.

For those who are interested in the relative abundance of the various forms, we have arranged the members of the family according to our concept of their status, beginning with the commonest and ending with the rarest.

<i>B. virginianum</i>	<i>B. lanceolatum</i> , subsp. <i>angustisegmentum</i>
<i>B. dissectum</i> , var. <i>obliquum</i>	<i>B. simplex</i> , var. <i>tenebrosum</i>
<i>B. dissectum</i> , var. <i>typicum</i>	<i>B. dissectum</i> , var. <i>oneidense</i>
<i>B. matricariaefolium</i>	<i>B. multifidum</i> , subsp. <i>siliafolium</i>
<i>O. vulgatum</i>	<i>B. simplex</i> , var. <i>laxifolium</i>

It is hoped that the present paper may be a stimulus to other local botanists in New Jersey to fill in the gaps in our distribution data and to check us on our taxonomical conclusions.<sup>3</sup>

BAILEY HORTORIUM,  
NEW YORK STATE COLLEGE OF AGRICULTURE,  
ITHACA, N. Y.

<sup>3</sup> Too late for inclusion in the text has come word of the collection by Mr. Bayard Long of *Botrychium simplex*, var. *tenebrosum* at Snyderstown in Hunterdon County, N. J. The plants from this collection have been examined by the senior author and are in every respect typical of the var. *tenebrosum*. This station represents not only our southernmost record for any form of *B. simplex* in New Jersey, but also for the entire eastern United States. The previous southernmost station for the var. *tenebrosum* was

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Pleasant Valley, Bucks Co., Pa. (B. Long 27329). Another New Jersey specimen of *B. simplex*, var. *laxifolium* has also come to our attention. This is the collection by Mr. Long, no. 8580, from moist maple woods near Big Spring at Springdale, in Sussex County.

While the type for this paper was being set up, the senior author had opportunity to study a small collection of specimens loaned through the kindness of Dr. G. A. Loughridge of the U. S. Soil Conservation Service. In this set were specimens of *B. dissectum*, var. *typicum* from two stations in Hunterdon County and of var. *obliquum* from one station in Somerset County. Among other collections that recently have been examined may be noted *B. multifidum*, ssp. *silvaifolium* from near Catfish Pond, Warren County (Fechtner) and *B. dissectum*, var. *obliquum* from Bergen Point, Hudson County. Dr. E. T. Wherry, in a recent letter, mentions a collection (Ph) of *B. simplex*, var. *laxifolium* from Geryville, Bucks Co., Pa. and of var. *tenebrosum* from Finland, Bucks Co., Pa., "a point along the west boundary of this county which proves to be a couple of miles farther south (as to latitude)" than the station at Snyderstown, N. J.

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Plate 7. Type collection of *Botrychium simplex*, var. *laxifolium*. No. 8 is the type specimen.



HERBARIUM OF ROBERT T. CLAUSEN, JR.  
FLORA OF NEW JERSEY  
No. 80  
*Botrychium simplex* E. Hitchc.  
Dry, shady woods, on limestone.  
Sporophylls slightly curved.  
Sporophylls on stipe. Part  
on the left. *Botrychium simplex*  
St. Edwards. *Botrychium simplex*  
C. T. CLAUSEN  
Johnsburg, June 24, 1935.



## Studies in Onagraceae X.<sup>1</sup> The subgenus *Kneiffia* (genus *Oenothera*) and miscellaneous new species of *Oenothera*

PHILIP A. MUNZ

A revision of the subgenus *Kneiffia* would seem rather superfluous because of the recent careful study by Pennell (Bull. Torrey Club **46**: 363-373. 1919), but it has been undertaken largely with the idea of bringing this group of species into a system consistent with the treatment of the rest of the genus. It has been my privilege recently to travel through the region where *Kneiffia* centers, in connection with the study being carried on by Professor Ralph E. Cleland and myself on the subgenus *Euoenothera* (*Onagra*) through the financial support of the Penrose Fund of the American Philosophical Society. It is a pleasure thus to acknowledge the aid given to an understanding of geographical distribution by seeing the habitat of the various species.

In connection with the preparation of this paper I have had the privilege of studying material in the following herbaria for which abbreviations used in citation of specimens are indicated in parentheses:

Botanisches Museum at Berlin-Dahlem (Ber),  
Boissier Herbarium at Geneva (Boiss),  
British Museum (BM),  
Delessert Herbarium at Geneva (Del),  
Gray Herbarium of Harvard University (G),  
Royal Botanical Garden of Kew (K),  
New York Botanical Garden (NY),  
Jardin des Plantes at Paris (Paris),  
Pomona College Herbarium (P),  
United States National Herbarium (US),

I am greatly indebted to the curators of these herbaria, particularly to those of Gray Herbarium for the privilege of use of the library as well as the herbarium, and to those at New York Botanical Garden for privileges extended in connection with the study of this and other groups of Onagraceae toward a treatment for the North American Flora.

### ***Kneiffia*** (Spach) new subgenus

*Kneiffia* as genus, Spach, Hist. Vég. Phan. **4**: 373. 1835 and Mon. Onagrearum, **44**. 1835; Raimann in Engl. & Prantl, Die Nat. Pflanzenfam. III, **7**: 214. 1893; Pennell, l.c.

*Kneiffia* as section, Endlicher, Gen. Pl., 1191. 1836-1840.

Plants caulescent herbs; buds mostly erect. Hypanthium cylindrical;

<sup>1</sup> No. IX of this series was published in Amer. Jour. Bot. **22**: 645-663. 1935.

flowers yellow, diurnal; stamens 8, the alternate ones longer; stigma with 4 linear lobes; fruit short, obovoid, tetragonal to 4-winged, narrowed into sterile pedicel-like base; seeds numerous, clustered in each cell, not in distinct rows, not angled nor tubercled.

Type species: *Kneiffia glauca* Spach, which is here treated as a synonym of *Oenothera tetragona* Roth var. *Fraseri* (Pursh) Munz.

#### KEY TO KNEIFFIA

Cauline leaves linear, 0.5–1 mm. wide; plants annual; floral bracts shorter than the capsules; hypanthium 1.5–2 mm. long; petals 3–5 mm. long; capsules ellipsoid, with ridge-like wings; stigma-lobes short and broad, not linear. §*Peniophyllum* (Pennell) n. sect.<sup>2</sup> 1. *Oe. linifolia*  
Cauline leaves broadly linear to ovate, usually more than 2 mm. wide; plants annual to perennial; floral bracts linear, often exceeding the capsules; hypanthium 4–18 mm. long; petals 5–25 mm. long; capsules clavate to oblong, with well defined wings; stigma-lobes elongate. §*Eukneiffia*, new section.

Plants annual; flowers in axils of ordinary foliage leaves of whole upper half of plant. La. & Tex. to Kans. 2. *Oe. Spachiana*

Plants perennial; flowers in axils of reduced leaves, hence in definite spikes, or simply in uppermost axils.

Buds and inflorescence erect; petals mostly 1 cm. or so long.

Capsule with no gland-tipped hairs, but with spreading or appressed non-glandular ones; capsule-body clavate-linear to -oblong.

Mature capsule clavate-linear, sessile, not narrowed into stipe-like base; sepals with free tips which are 1–4 mm. long.

Plant with long spreading hairs 1–2 mm. long; capsule 10–20 mm. long; hypanthium 15–25 mm. long. Mo. to Ia., Mich., Ohio; occasional farther east. 3. *Oe. pilosella*

Plant with shorter appressed hairs not more than 1 mm long; capsule 8–10 mm. long; hypanthium 10–17 mm. long. La. to Ark. 4. *Oe. sessilis*

Mature capsule clavate, narrowed into a sterile stipe-like base; sepal-tips not free, or if so, less than 1 mm. long. 5. *Oe. fruticosa*

Capsule with gland-tipped hairs, only, or occasionally with some non-glandular ones in addition; capsule-body tending to be oblong to oblong-ellipsoid. 6. *Oe. tetragona*

Buds and tip of inflorescence nodding; petals 5–10 mm. long. 7. *Oe. perennis*

#### TREATMENT OF SPECIES

1. *OENOTHERA LINIFOLIA* Nutt., Journ. Acad. Philad. 2: 120. 1821.

*Kneiffia linifolia* Spach, Nouv. Ann. Mus. Paris 4: 368. 1835. *K. lineari-folia* Spach, Ann. Sci. Nat., Sér. II, 4: 167. 1835. *Peniophyllum linifolium* Pennell, Bull. Torrey Club 46: 373. 1919.

Erect annual, with slender stems 1–3 dm. high, simple or with few ascending branches usually near the middle (occasionally at the base), plant as whole glabrous or with few soft hairs, inflorescence puberulent; basal leaf-blades ovate to oblanceolate, 1–2 cm. long, petioled, dying early; cauline leaves numerous, linear to filiform, 1–2.5 cm. long, subsessile, ascending, persistent; flowers few, in terminal spikes; bracts ovate to deltoid-ovate, 2–4 mm. long; hypanthium 1.5–2 mm. long; sepals reflexed in pairs, 1.5–2 mm. long, without

<sup>2</sup> *Peniophyllum* as genus, Pennell, Bull. Torrey Club 46: 373. 1919.

free tips, somewhat reddish, puberulent; petals 3-5 mm. long, obcordate; filaments glabrous, unequal, about half as long as petals; anthers glabrous, oblong, 1-1.5 mm. long; style glabrous, extending about as far as do the filaments; stigma 1 mm. broad, shallowly and broadly lobed; capsule ellipsoid, sessile, 4-6 mm. long, 4-angled; seeds brown, ca. 1 mm. long, somewhat angled, ellipsoid.

## KEY TO VARIETIES

Inflorescence strigulose-puberulent but scarcely or not at all glandular. Ala. to Miss. Valley.

1a. var. *typica*

Inflorescence not strigulose but glandular-puberulent. Ga.

1b. var. *glandulosa*

1a. *Oenothera linifolia* Nutt. var. *typica* n. nom.

*Oe. linifolia* Nutt., l. c.

Type locality, "near the banks of the Arkansa," Nuttall. Representative material, ALABAMA: Auburn, *Earle in 1901* (NY). LOUISIANA: Natchitoches, *Palmer 7368* (NY, US); Fisher, *Benke 5531* (P, US); Opelousas, *Langlois in 1880* (NY). MISSOURI: Webb City, *Palmer in 1903* (G, NY); Nichols Junction, *Bush 260* (G, NY, US); Allenton, *Letterman in 1882* (G, NY, US). ILLINOIS: Tunnell Hill, Johnson Co., *Seymour in 1882* (G); Makanda, *Gleason in 1903* (G). ARKANSAS: *Oenothera linifolia*, Arkansas, Nuttall, type coll. (BM, NY, K); Prescott, *Bush 249* (G, K, NY, US); Hot Springs, *Scully 238* (P); Fulton, Hempstead Co., *Palmer 5404* (P, US). KANSAS: Chautauqua Co., *Hitchcock 688a* (G, NY, Paris, US); Caney, *Rydberg & Imler 426* (NY). OKLAHOMA: Page, LeFlore Co., *Stevens 1395* (G, NY, K, US); Sapulpa, *Bush 166* (G, NY, US), *1191* (Ber, NY, K). TEXAS: Galveston Bay, *Drummond 78* (BM, G, K, NY); Galveston, *Lindheimer 54* (Ber, BM, G, K, Paris); Houston, *E. Hall 210* (BM, G, K, NY, P, US).

1b. *Oenothera linifolia* Nutt. var. *glandulosa* n. var.

Inflorescentia glandulosa-puberulenta, non strigulosa.

Type from Little Stone Mt., DeKalb Co., Ga. *Curtiss 6778* at Gray Herb., isotypes at Del, K, NY, Paris, US. Other material seen, GEORGIA: Athens, *Perry 966* (P); rocky base of Pine Mt. north of Lithonia, *Perry & Meyers 967* (G); Little Stone Mt., *Biltmore Herbarium 5703* (BM, G, NY, US).

2. OENOTHERA SPACHIANA Torr. & Gray. F1. No. Am. 1: 498. 1840.

*Kneiffia Spachiana* Small, Bull. Torrey Club 23: 179. 1896. *Oenothera fruticosa* "race" *Spachiana* Léveillé, Monogr. Oenothera, 106, pl. 13. 1902. *Blennoderma Drummondii* Spach, Nouv. Ann. Mus. Paris 4: 407. 1835. *Oenothera Drummondii* Walp., Rep. 2: 85. 1843, not Hooker, 1834. *Oe. uncinata* Scheele, Linnaea 21: 578. 1848.



Annual, erect; stem slender, simple or with few ascending branches, 1-3 dm. high, strigose throughout; basal leaf-blades ovate to oblanceolate, subentire, 2-4 cm. long, petioled; cauline leaves mostly oblong-lanceolate to oblong-linear, obtuse, subentire, 3-5 cm. long, 4-8 mm. wide, gradually narrowed into short petioles; flowers in leaf-axils from about the middle of the plant; hypanthium slender, strigose, 4-6 mm. long; sepals 8-10 mm. long, green, strigose, 4-6 mm. long; sepals 8-10 mm. long, green, strigose, reflexed in pairs or 4's at anthesis, with narrowed subulate but connivent tips 1-1.5 mm. long; petals obovate, 5-15 mm. long, somewhat emarginate, with reddish veins in age; filaments unequal, whitish, about half the petals in length, glabrous; anthers oblong-linear, 2-3 mm. long, yellow; style glabrous, slightly exceeding stamens; stigma cylindric-clavate, the 4 somewhat elongate lobes apparently connivent; capsule indurate, broadly clavate, 4-winged, strigose, 3-4 mm. wide and 8-10 mm. long, narrowed at the sterile sessile base; seeds straw-color, 0.6 mm. long, sharply angled.

Type locality, "Texas," Drummond. Representative material, LOUISIANA: locality uncertain, *Hale* (NY); Opelousas, no collector given (US). ARKANSAS: Fulton, *Bush* 1428 (G, NY, US), *Palmer* 5817 (P, US). OKLAHOMA: Weoka, *Carleton* 111 (US); Atoka, *Oyster in* 1883 (US); Manns-ville, *Griffith* 3486½ (G, NY). TEXAS: Houston, *E. Hall* 206 (BM, G, K, NY, P, US); without locality, *Drummond* 81 (Del, G, K); Dallas, *Reverchon* 912 (G, K, NY, US); Columbia, *Bush* 73 (G, K, NY, US), 469 (G, K, NY, US); San Augustine, *Palmer* 7897 (NY, US).

3. *OENOTHERA PILOSELLA* Raf., Ann. Nat., 15. 1820.

*Kneiffia pilosella* Heller, Cat. No. Am. Pls., ed. II, 8. 1900. *K. fruticosa* var. *pilosella* Britton, Mem. Torrey Club 5: 234. 1894. *Oenothera fruticosa* var. *pilosella* Small & Heller, Mem. Torrey Club 3: 26. 1892. *Oenothera fruticosa* var. *hirsuta* Nutt. ex Torr. & Gray, Fl. No. Am. 1: 496. 1840. *Oe. fruticosa* f. *hirsuta* Lévl., Mon. Onoth., 108. 1902. *Kneiffia pratensis* Small, Fl. S. E. U. S., 842, 1335. 1903. *K. Sumstinei* Jennings, Ann. Carnegie Mus. 3: 480, pl. 19. 1906.

Perennial; stems apparently from short rootstocks, erect, simple, or few-branched above, 1.5-6 dm. tall, reddish, spreading-hirsute, the hairs mostly 1-2 mm. long and somewhat tawny; basal leaves apparently obovate to oblanceolate, long-petioled; cauline leaves gradually reduced up the stem, lanceolate to almost ovate, sessile to short-petioled, 2-10 cm. long, 0.8-2.5 cm. wide, obtusish, minutely and irregularly denticulate, more or less hirsute; flowers several; hypanthium slender, 15-25 mm. long; sepals green, reflexed in 2's or 4's at anthesis, 10-20 mm. long, more or less hirsute, the divaricate subulate tips 1-3 mm. long; petals obcordate, 13-25 mm. long, conspicuously veined; filaments somewhat unequal, half the length of the petals, glabrous; anthers 5-8 mm. long; style retrorse-puberulent in the lower part of the hy-

panthium, equal to or slightly exceeding the stamens; stigma-lobes linear, 2-4.5 mm. long; capsule sessile, linear-clavate, hirsute, 10-20 mm. long, 2-3 mm. thick; seeds not seen.

Type locality, near Evansville, Indiana. Rafinesque's description of *Oe. pilosella* seems to me to refer distinctly to the plant which has in recent years gone under the name of *Oe. pratensis*. Therefore even though I have not seen a Rafinesque type, I take up his name. The species is common enough in Indiana where Rafinesque secured his type. Through the kindness of Mr. C. C. Deam of Bluffton, Ind. I have had the privilege of examining over thirty collections from that state. The species ranges from Mo. and Ia. to Wis. and the Ohio River drainage. I presume the occasional plants found farther east are adventive (cf. Wiegand & Eames, Fl. Cayuga Lake Basin, 316, 1925). I wish to acknowledge the kindness of Drs. Jennings and Graham of the Carnegie Museum of Pittsburg in lending me the type of *K. Sumstinei*.

Representative material, MISSOURI: St. Louis, *Engelmann in 1845* (Ber), *Riehl* (K, Paris); Allenton, *Letterman in 1894* (US). IOWA: Johnson Co., *Somes 3195* (US); Winfield near Burlington, *Gambell in 1894* (G). ILLINOIS; without locality, *Oe. fruticosa*  $\sigma$  *hirsuta*, *Nuttall* (BM, NY); Kankakee, *Crampton 127* (US); Joliet, R. R., *Boott in 1859* (G); Walden, *Harper in 1893* (P); Newton, Jasper Co., *Stout in 1927* (P). INDIANA: 3 mi. NW. of Leavenworth, Crawford Co., *Deam 20438* (G, NY); 2 mi. S. of Conrad, Newton Co., *Deam 48906* (G, Deam Herb.). MICHIGAN: Washington, *Farwell 5887* (G); Alganac near Port Huron, *Dodge 92* (NY, US). OHIO: Oberlin, *Ricksecker in 1895* (US); Richland Co., *Wilkinson in 1892* (NY). PENNSYLVANIA: Kittanning, *Sumstine in 1905*, type coll. K. Sumstinei (NY, Carnegie Mus.); West Chester, *Townsend 9* (K). NEW YORK: Montezuma Village, *Eames, Randolph & Wiegand 12617* (G, Deam Herb.); Randolph, *Limberger in 1908* (G). ONTARIO: Port Franks, Lambton Co., *Dodge 272* (US). MAINE: Hartford, *Parlin in 1884* (G). MASSACHUSETTS: So. Lincoln, *Farrar in 1891* (G). VIRGINIA: *Vasey in 1884* (US).

#### 4. *Oenothera sessilis* (Pennell) n. comb.

*Kneiffia sessilis* Pennell, Bull. Torrey Club 46: 366. 1919.

Much like *Oenothera pilosella*, but strigose with shorter ascending hairs; hypanthium 10-17 mm. long; free sepal-tips 1-2 mm. long; petals 10-20 mm. long; capsule strigose, 8-10 mm. long.

Type locality, Little Rock Ark. A comparatively little known plant, apparently amply distinct from *Oe. pilosella* in the very short appressed pubescence, and from *Oe. fruticosa* in the narrower, more elongate capsule. Specimens seen. LOUISIANA: Alexandria, *Hale* (G, US). ARKANSAS: Little

Rock, *Hasse, June 2, 1885*, type (NY); Sebastian Co., *Palmer 39308* (G); prairies, E. Ark., *Harvey 16* (G). The following collections resemble *Oe. sessilis* and *Oe. pilosella* in the yellowish pubescence and *Oe. fruticosa* in the stipitate condition of the capsules, ARKANSAS: Benton Co., *Plank in 1899* (NY); Little Rock, *Hasse, May, 26, 1885* (NY). Other specimens nearer to *Oe. fruticosa* are discussed under that species.

5. *OENOTHERA FRUTICOSA* L., Sp. Pl., 346. 1753.

Perennial herb; stems erect or ascending or spreading, simple or branched, 1-6 dm. tall, variously pubescent; basal leaf-blades ovate to spatulate, sub-entire to undulate-toothed, commonly 1-5 cm. long, on petioles almost as long; cauline leaves mostly lanceolate, sometimes almost linear, 2-7 cm. long, sessile or short-petioled, entire to remotely denticulate, gradually reduced up the stem, the uppermost becoming linear bracts 1-2 cm. long; inflorescence more or less pedunculate; flowers more or less crowded at summit of main stem or its branches; hypanthium slender, 5-15 mm. long; sepals lanceolate, 5-20 mm. long, usually reflexed in 4's at anthesis, with narrow tips up to about 1 mm. long, these not free or, if free, not strongly divaricate; petals obovate, 1-2.5 cm. long, usually shallowly toothed; filaments somewhat unequal, glabrous, almost half the length of the petals; anthers 4-6 mm. long; style retrorsely puberulent on lower part within the hypanthium, slightly exceeding the stamens; stigma-lobes linear, 1.5-3 mm. long; capsule more or less clavate, the body proper subglobose to obovoid and narrowed basally into a sterile stipe-like part, sessile or pediceled; seeds sharply angled, brown or black, about 0.6 mm. long.

KEY TO VARIETIES

Stems ascending to erect, mostly 3-7 dm. long, simple or branched above.

Capsule-body proper 6-9 mm. long, with rather coarse pubescence.

Pubescence especially of capsules and pedicels appressed.

5a. var. *vera*

Pubescence of capsules and pedicels spreading.

5b. var. *vera* f. *angustifolia*

Capsule-body proper 4-5 mm. long, with very fine and minute puberulence.

Georgia and Alabama.

5c. var. *subglobosa*

Stems diffusely spreading, 1-2 dm. long, much branched.

Capsule-body strigulose, 6-8 mm. long. Long Island.

5d. var. *humifusa*

Capsule-body 10 mm. long, with short spreading hairs. Connecticut.

5e. var. *Eamesii*

5a. *OENOTHERA FRUTICOSA* L. var. *VERA* Hook., Bot. Mag. 64: with pl. 3545. 1837.

*Oenothera fruticosa* L., Sp. Pl., 346. 1753. *Oe. florida* Salisb., Prodr., 278. 1796, new name for *fruticosa*. *Kneiffia suffruticosa* Spach, Hist. Vég. Phan. 4: 374. 1835, new name for *fruticosa*.

Stems simple to paniculately or cymosely few-branched above, more or less strigulose, 3-7 dm. high, erect or ascending; basal leaf-blades oblanceolate to almost obovate, 2-7 cm. long, petioled, denticulate; lower cauline leaves lanceolate, 2-8 cm. long, 7-12 mm. wide, short-petioled, uppermost reduced,

mostly lanceolate, all more or less strigulose; fruiting "pedicels" mostly 5-12 mm. long, strigulose; capsule-body strigose, 6-9 mm. long, 2-3 mm. wide.

Type locality, Virginia, taking as type *Clayton 36* (BM). I have seen the material in the Linnean Herbarium and at the British Museum and agree in interpretation of the type with Blake, *Rhodora* 20: 51. 1918 and with Pennell, *Bull. Torrey Club* 46: 367. 1919. The var. *vera* apparently ranges from Barnstable Co., Mass. to Fla., apparently being confined closely to the Atlantic row of states. Representative material, *Oe. fruticosa*  $\beta$  Hook., *H. Gl.*, N. Am., *Herb. Hook.* (K); *Oe. hybrida*, *Cobham Lodge, June 1826*, *Herb. Forbes Young* (K); *Oe. linearis*, *affinis Onagrae, Clayton No. 491*, *Michaux Herb.* (Paris). MASSACHUSETTS: West Harwich, Barnstable Co., *Fernald & Long 17215* (G, NY, US). CONNECTICUT: Westport, *Eames in 1901* (G); New Haven, *Eaton in 1858* (G). NEW YORK: Montauk, L. I., *Ferguson in 1918* (NY, P); Penn Yan, Yates Co., *Wright* (P). NEW JERSEY: Atlantic City, *Hunnewell 6026* (G); Plainfield, *Drushel 6805* (US); Cape May, *Boott in 1860* (G). PENNSYLVANIA: Pleasant Grove, *Carter in 1908* (NY); Marysville, Perry Co., *Small in 1888* (NY). DELAWARE: New-castle, *Canby in 1863* (G); Woodland Beach, *Commons in 1880* (NY). MARYLAND: Hyattsville, *Steele in 1916* (P); Easton, *Clark 2* (G), *Shreve 180* (US). VIRGINIA: Fredericksburg, *Munz 1566* (P); Occoquan, Fairfax, Co., *L. F. & F. R. Randolph 165* (G). WEST VIRGINIA: Long Glade, Webster Co., *Millsbaugh 579* (NY). NORTH CAROLINA: Olympia, *L. F. & F. R. Randolph 916* (G); Biltmore, *Biltmore Herb 669* (NY, US); Statesville, *Hyams* (P, US); Winfall, *Wiegand & Manning 2213* (G). SOUTH CAROLINA: Marion, *Wiegand & Manning 2219* (G); Burgess P. O., Horry Co., *Weatherby & Griscom 16595*, with unusually narrow leaves (G, NY, US). GEORGIA: Stone Mt., *Eggert in 1897* (NY); Savannah, *Harper in 1844*, leaves almost linear (Paris). FLORIDA: Mt. Vernon, *Chapman* (G); Aspalaga, *Curtiss 909* (G, K, BM, Ber, NY, P, US).

Some collections from the southern part of the range vary toward *Oe. tetragona* in the presence of some gland-tipped hairs on the capsules: near Wilmington, N. Car., *Wiegand & Manning 2218* (G).

5b. *OENOTHERA FRUTICOSA* var. *VERA* forma *ANGUSTIFOLIA* Lévl., *Mon. Onoth.*, 108, oppos. pl. 14. 1902.

*Kneiffia angustifolia* Spach, *Nouv. Ann. Mus. Paris* 4: 367. 1835, new name for *Oe. linearis*. *Oenothera fruticosa* var. *angustifolia* Spach ex Lévl., l.c., pl. 14. *Oenothera linearis* Michx., *Fl. Bor. Am.* 1: 225. 1820. *Oe. fruticosa* var. *linearis* Wats., *Proc. Amer. Acad.* 8: 584. 1873. *Kneiffia linearis* Spach *Hist. Vég. Phan.* 4: 376. 1835. *Oenothera fruticosa* var. *linearifolia* Hook., *Bot. Mag.* 64: with pl. 3545. 1837. *Kneiffia longipedicellata* Small, *Bull. Torrey Club* 23: 178.

1896. *Oenothera longipedicellata* Robinson, *Rhodora* 10: 34. 1908. *Kneiffia arenicola* Small, Fl. S. E. U. S., 842, 1335. 1903. *Oenothera arenicola* Coker, Pl. Life of Hartsville, 94. 1912. *Oe. subglobosa* var. *arenicola* Weatherby & Griscom, *Rhodora* 36: 48. 1934. *Oe. fruticosa* var. *differta* Millsp., Fl. W. Va., 366. 1892. *Kneiffia fruticosa* var. *differta* Millsp., Living Fl. W. Va., 312. 1913. Apparently *Oe. fruticosa* f. *diversifolia* Lévl., l.c., 108.

Like var. *vera*, but with spreading pubescence especially on capsules and pedicels.

Type locality, North Carolina. The name *angustifolia* is used as the first one of rank of form; it is based on the same type as that of *linearis* in the description of which Michaux cites two specimens: the first one "*Oe. linearis*, Pluk. t. 426. f. 6, cette Echantill. se rapporta à la phrase de Pluknet é tant glabre," Michx. Herb. (Paris) I take as the type. The second one cited, *Clayton 491* (Paris), is strigose and is var. *vera*, as here treated. I use the rank of form rather than variety for the group under consideration because plants with appressed pubescence and those with spreading hairs grow together so freely and there seems to be no difference in range. Intergrades between the var. *vera* and the forma *angustifolia* are not uncommon; the pubescence not only of the stems but even of the fruits may be quite intermediate, for example, Derby, Conn., *Eames in 1895* (US); High Point, N. Car., *Kennedy in 1885* (G); Montgomery, Ala., *Alphonse Wood* (NY).

I am greatly indebted to Prof. P. S. Strausbaugh of the University of West Virginia for a photograph of and notes on the type of *Oe. fruticosa* var. *differta*; this specimen from Kanawha Station, Wood Co., *Millsbaugh 286* reveals nothing that in my opinion warrants varietal recognition. Nor can I find anything consistent in length of pedicel for recognition of *longipedicellata* nor in the roundness of the capsule for maintaining *arenicola*. Representative material of forma *angustifolia* may be cited as follows: MASSACHUSETTS: West Harwich, *Fernald & Long 17216* (G, NY, US). CONNECTICUT: Stratford, *Eames 176* (G); Southbury, *Blewitt 63* (G). NEW YORK: Montauk. L. I., *Ferguson in 1920* (NY, P); Staten Island, *Crooke in 1868* (NY). PENNSYLVANIA, Pleasant Grove, Lancaster Co., *Heller in 1901* (Ber, US). NEW JERSEY: Penns Grove, *Meredith in 1921* (G, NY); Milburn, *Mackenzie 2147* (NY). MARYLAND: Cabin John, Montgomery Co., *House 293* (NY); Riversdale, *Steele in 1916* (G). VIRGINIA: Alexandria, *Wiegand & Manning 2211* (G, P); Flat Rock, *Davis 1497* (US); Raleigh, *Biltmore Herb. 6045d* (US). NORTH CAROLINA: Enfield, *Prior in 1849* (K); Statesville, *Hyams* (P). SOUTH CAROLINA: Tomassee, Oconee Co., *House 2015* (US). GEORGIA: Warm Springs, *Tracy 9272* (BM, Del, G, NY, US); Statesboro, *Harper 2164* (Ber, Edinburgh, G); Sandhills,

Augusta, *Biltmore Herb.* 5649d, type *arenicola* (NY). FLORIDA: Chipley, *Small & Wherry* 11693 (NY); Ellaville, Madison Co., *Moldenke* 1106 (NY). ALABAMA: Auburn, *Earle* 2063 (NY, US), *Earle & Baker*, April 24, 1897 (P, US).

Much farther west is a form which seems very close to *angustifolia* and yet in the coarseness and character of pubescence approaches *Oe. pilosella*. More material of this is desirable; such are plants from Seligman, Mo., *Bush* 263 (G, K, NY, US); Eagleton, Ark., *Benke* 5499 (P, US); Mena, Ark., *Howell* 665 (US); Page, Okla., *Stevens* 1410 (Del, G); Pittsburg Co., Okla., *McClary in* 1935 (P). The best disposition that I can now make of them is to say that they seem intermediate between *Oe. pilosella* and *Oe. fruticosa* especially of the form *angustifolia*.

5c. *Oenothera fruticosa* L. var. *subglobosa* (Small) n. comb.

*Kneiffia subglobosa* Small, Bull. Torrey Club **23**: 177. 1896. *Oenothera subglobosa* Weatherby & Griscom, *Rhodora* **36**: 48. 1934.

Stems several, ascending to erect, 3–8 dm. high, strigulose, freely branched above; basal leaves narrowly oblanceolate, 3–8 cm. long, 4–9 mm. wide, remotely denticulate, sparingly strigulose beneath, on petioles up to 2 cm. long; cauline leaves mostly almost linear; hypanthium and calyx very finely strigulose; capsule-body 4–5 mm. long, very finely strigulose, the pedicel and narrow base 5–20 mm. long.

Type locality, Stone Mt., DeKalb Co., Ga. Representative material, GEORGIA: Stone Mt., *Small in* 1894, type (NY), *Wiegand & Manning* 2228 (G), *Curtiss* 6472 (Del, G, K, NY, Paris, US), *Harper* 172 (Ber, BM, G, K, NY, US); Lithonia, *Pollard & Maxon* 504 (NY, US). ALABAMA: Auburn, Lee Co., *Earle & Earle* 48 (NY, US), *Munz* 1332 (P).

The following plants have the fine pubescence of *subglobosa*, but the elongate capsule-bodies (6–8 mm.) of *vera*: Stone Mt., Ga., *Eggert in* 1897 (NY, US), *Perry* 969 (G, US); Auburn, Ala., *Earle & Baker* 1622 (NY). Nor can *subglobosa* be separated by its narrow leaves, since the leaves of *vera* tend to be so in the southern part of its range.

5d. *OENOTHERA FRUTICOSA* L. var. *HUMIFUSA* Allen, Bull. Torrey Club **1**: 3. 1870.

*Kneiffia fruticosa humifusa* Pennell, Bull. Torrey Club **46**: 368. 1919. *K. linearis Alleni* Britton, Mem. Torrey Club **5**: 235. 1894. *K. Alleni* Small, Bull. Torrey Club **23**: 177. 1896.

Stems slender, 1–2 dm. long, freely branched, densely leafy, diffusely spreading; plants strigose throughout; leaf blades oblanceolate to oblong-lanceolate, 1–3 cm. long, entire to irregularly denticulate, mostly obtuse, on petioles 1–6 mm. long; fruiting pedicels 5–12 mm. long; capsule proper strigulose, 6–8 mm. long.

Type locality, Montauk Point, Long Island, N.Y. Material representative, LONG ISLAND: Montauk Point, *Allen in July, 1869*, type coll. (G, NY), *Miller & Allen in 1878* (NY, P, US); Auerbachs, *Bicknell in 1908* (NY); Greenport, *Lowerre in 1897* (G); East Hampton, *Wheelock in 1890* (NY); Shinnecock Bay, *Howell in 1898* (US). Long Island plants are very closely approached in habit by some from NEW JERSEY: Seaside Park, *Drushel 7295* (US); Barnegat Pier, Ocean Co., *Mackenzie 3718* (NY, US).

Long Island specimens quite intermediate in stature and size between *humifusa* and *vera* are: Southampton, *Chute in 1899* (NY); East Rockaway, *Britton & Mulford in 1902* (NY); Long Beach, *Bicknell in 1906* (NY); Springfield, *Bicknell in 1902* (NY).

5e. *OENOTHERA FRUTICOSA* L. var. *EAMESII* (Robinson) Blake, *Rhodora* 20: 51. 1918.

*Oe. linearis* var. *Eamesii* Robinson, *Rhodora* 10: 34. 1908.

With general aspect and habit of var. *humifusa*, but with the capsule-body about 10 mm. long and with spreading hairs.

Type locality, Stratford, Stratford Co., Conn. Material seen, CONNECTICUT: Stratford, *Eames in 1896*, type (G), *in 1898* (G), *171a*, *in 1901* (G).

6. *OENOTHERA TETRAGONA* Roth, *Catalecta Bot.*, fasc. 2: 39. 1800.

Perennial; stems ascending to erect, 2-10 dm. high, mostly simple below, simple or branched above, glabrous to strigose to pubescent; basal leaf-blades spatulate to ovate, 1-10 cm. long, subentire to denticulate, on petioles up to their own length; cauline leaves lance-linear to ovate, 1-10 cm. long, gradually shorter and with decreasing petioles upward; uppermost reduced to linear or ovate-lanceolate bracts, these from less than to exceeding the capsules; inflorescence few-flowered, compact at the ends of the branches, more or less pedunculate; hypanthium and ovary glandular-puberulent, rarely with other hairs, or rarely even subglabrous; hypanthium slender, 6-15 mm. long, often reddish; sepals 8-18 mm. long, with or without long narrow tips which are often connivent in the bud, sometimes free for the last mm.; petals 10-30 mm. long, obovate, more or less notched; filaments somewhat unequal, glabrous, about half the petals; anthers glabrous, 4-8 mm. long; style puberulent at base within hypanthium; stigma-lobes linear, 2-4 mm. long; capsule-body ellipsoid-oblong, to -clavate, 6-15 mm. long, narrowed into a shorter or equally long narrow stipitate portion; seeds brown, 0.6-1.0 mm. long, scarcely to definitely angled.

#### KEY TO VARIETIES

Capsule and ovary with glandular hairs only.

Petals mostly less than 2 cm. long; cauline leaves lanceolate to lance-linear, mostly less than 15 mm. wide, not glaucous beneath.

- Pubescence of stems spreading. 6a. var. *typica*  
 Pubescence of stems appressed. 6b. var. *longistipata*  
 Petals mostly 2.5-3 cm. long; cauline leaves lance-ovate to ovate, 1-3 cm. wide, glaucous beneath.  
 Plant glabrous. 6d. var. *Fraseri*  
 Plant not glabrous.  
 Stems with spreading hairs. 6e. var. *Fraseri* forma *hybrida*  
 Stems with appressed hairs. 6f. var. *Fraseri* forma *latifolia*  
 Capsule and ovary with some non-glandular hairs among the glandular ones, or almost glabrous.  
 Leaves soft-pubescent. Hempstead Plain, Long Island, New York. 6c. var. *celutina*  
 Leaves not soft-pubescent. Carolina and Tennessee southward.  
 Cauline leaves mostly less than 6 cm. long and less than 6 mm. wide; petals 1-2 cm. long; capsule-body 5-8 mm. long. Tenn. to Ga. & La. 6g. var. *brevistipata*  
 Cauline leaves 5-12 cm. long, 5-15 mm. wide; petals 1.5-3 cm. long; capsule-body 8-12 mm. long. Wilmington, N. Car. 6h. var. *riparia*

6a. *Oenothera tetragona* Roth var. *typica* n. nom.

*Oe. tetragona* Roth, Cat. Bot., fasc. 2: 39. 1800. *Kneiffia tetragona* Pennell, Bull. Torrey Club 46: 370. 1919. *Oenothera fruticosa* var. *ambigua* Nutt., Gen. No. Am. Pls. 1: 247. 1818. *Oe. ambigua* Spreng., Syst. 2: 229. 1825, apparently same as Nuttall's, but does not refer to it. *Oe. hybrida* var. *ambigua* Blake, Rhodora 20: 52. 1918. Probably *Oenothera incana* Nutt., Gen. No. Am. 1: 247. 1818. Probably *Oe. fruticosa* var. *incana* Hook., Bot. Mag. 64: with pl. 3545. 1837. *Oe. fruticosa* var. *phyllopus* Hook., l.c. Probably *Oe. fruticosa* var. *indica* Lindl., Bot. Reg. 27: pl. 11. 1841. Apparently *Oe. canadensis* Goldie in Edinb. Phil. Journ. 6: 325. 1822.

Stems with short spreading pubescence, sometimes almost glabrous; cauline leaves lanceolate, 2-7 cm. long, 5-10 (15) mm. wide; petals 12-20 (25) mm. long; mature capsules with spreading gland-tipped hairs, oblong, the body proper 5-9 mm. long, 2.5-3 mm. wide (including wings), rather abruptly narrowed at base, sessile or on short pedicels scarcely distinguishable from the stipe-like base; seeds brown, scarcely angled, 0.6 mm. long.

Type locality not given. I have seen what I take to be the type: "Ex horto meo Vegesackii, 1799, *Oe. tetragona*, Herb. A. W. Roth" (Ber, photo at P). Nuttall's var. *ambigua* seems to belong here, judging from the description which emphasizes the oblong capsules, spreading hair of the stems, and habitat as about Philadelphia. Blake, Rhodora 20: 52. 1918, arrives at the same conclusion, namely that it is not in *Oe. fruticosa*. I have not seen Nuttall's type. At the British Museum is a sheet labeled "Oenothera ambigua, *Oe. fruticosa* ambigua Gen. Am., Cambridge, Mass., Nuttall," but there is no asterisk before the word "ambigua" which Nuttall would have used had it been the type, the place is Cambridge and not Philadelphia; and the sheet contains two specimens, one of which is *Oe. perennis*, the other is *Oe. fruticosa* L., with pubescent, not glandular capsules. Nor have I seen Nuttall's type of *Oe. incana*, but place it here be-



cause of the description. Hooker's var. *phyllopus* refers to Curtis Bot. Mag., pl. 332, which is an excellent illustration of *tetragona typica*. Goldie's *canadensis* is based on a collection from the "Island of Montreal," which seems away out of the range of *tetragona*; however, the description and a specimen "Canada," Goldie (K) which may or may not be the type collection are unquestionably *tetragona*. The only specimen I have seen of Lindley's *indica* "Garden, July 1839, d. Lindley" (Ber) and the description and plate lead to my reduction to synonymy here.

Just what the original geographical limits of *tetragona typica* may have been, I do not know. I have seen material from Nova Scotia to Georgia and Tennessee. Representative material, NOVA SCOTIA: Ashmore, Digby Co., *Fernald & Long 24215* (G, NY). MAINE: Alton, *Fernald in 1900* (G); Pembroke, *Fernald in 1897* (G). NEW HAMPSHIRE: Derry, *Seaman* (US). NEW YORK: Loch Muller, Essex Co., *House 15742* (G); Bronx Park, *Bicknell 301* (NY); Staten I., *Britton in 1879* (G). PENNSYLVANIA: between Churchtown & Beartown, Lancaster Co., *Heller 549* (Boiss, G, NY, US); Naomi Pines, Pocono Plateau, Monroe Co., *Britton in 1893* (NY). NEW JERSEY: Harrington Park, *Pollard in 1893* (P, US); Boardville, Passaic Co., *Mackenzie 2733* (NY). DELAWARE: Wilmington, *Tatnall* (G). MARYLAND: Hog Hills, Cecil Co., *Shreve 362* (US). VIRGINIA: Clarendon, *Blake 10602* (P); Giles Co., *Meredith in 1923* (P). SOUTH CAROLINA: Clemson, Pickens Co., *House 3340a* (NY); Batesburg, Lexington Co., *McGregor 168* (US). GEORGIA: Louisville, *Hopkins* (NY). KENTUCKY: Mammoth Cave, *Palmer in 1899* (US). TENNESSEE: Knoxville, *Ruth in 1895* (NY); Tullahoma, Coffee Co., *Eggert in 1897* (US).

6b. *Oenothera tetragona* Roth var. *longistipata* (Pennell) n. comb.

*Kneiffia tetragona* var. *longistipata* Pennell, Bull. Torrey Club 46: 371. 1919. *Oenothera serotina* Sweet, Brit. Fl. Garden, ser. 1, 2: pl. 184. 1826. *Oe. serotina* Lehm., Sem. Hort. Hamb. (1825), 17 and Linnæa, Litteraturbericht, 10, 1828 seems same as that of Sweet. *Kneiffia maculata* Spach, Hist. Vég. Phan. 4: 375. 1835, new name for *serotina*.

Like var. *typica*, but with appressed stem-pubescent.

Type locality, "woods near Clemson, Pickens County, South Carolina." My use of this variety is quite different from Pennell's, being based on appressed pubescence rather than length of stipe. I recognize this as a variety instead of a form, because of the distinctly more western range. While *typica* is occasional in the more southern part of its range, this variety is more abundant there, and seems to be most frequent in the Ohio River drainage.

*Oe. serotina* was figured by Sweet as having spreading hairs, but the

only early and therefore probably authentic specimens I have seen are all strigose. "Oe. serotina, rec'd from London Garden in 1825, no. 15, Herb. Hook." (K); "Oe. serotina, Cobham Lodge, July 1826, Lee" (K); "Oe. serotina, garden of Edw. Leeds" (K).

I have seen material distributed as follows, NEW YORK: Quakers Bridge, Alleghany State Park, Cattaraugus Co., *Alexander & House 12242* (G); Grassy Sprain Lake, Westchester Co., *Bicknell in 1898* (NY). PENNSYLVANIA: mouth of Tucquan, Lancaster Co., *A. A. & E. G. Heller 1341* (G); Fern Hill, Chester Co., *Bartram in 1910* (G). WEST VIRGINIA: White Sulphur Springs, *Hunnewell in 1914* (G). MARYLAND: Oakland, Garrett Co., *Smith in 1881* (US); Big Savage Mt., Garrett Co., *Shreve 850* (US). VIRGINIA: Hot Springs, Bath Co., *Hunnewell 4727* (G); Great Falls, Fairfax Co., *Hunnewell 5414* (G). NORTH CAROLINA: Montreat, Buncombe Co., *Standley & Bollman 10142* (US); Kings Mt., *Biltmore Herb. 6045f* (US). SOUTH CAROLINA: Clemson, *House 3340*, type longistipata (NY); Hartsville, *Coker in 1909* (NY); Batesburg, Lexington Co., *McGregor 116* (US), *624* (US). GEORGIA: Rome, *Biltmore Herb. in 1899* (US); Augusta, *Cuthbert 934* (NY). MICHIGAN: Olivet, *McClatchie in 1887* (US); Kalamazoo, *Tuthill in 1873* (G). OHIO: Kimball, Erie Co., *Moseley in 1897* (G, US); Cleveland, *Krebs 563* (Ber). INDIANA: near Ora, Starke Co., *Deam 49016* (G, Herb. Deam); near San Pierre, Pulaski Co., *Deam 43240* (G, Herb. Deam); near Kniman, Jasper Co., *Deam 48920* (G, Herb. Deam). KENTUCKY: Paducah, *Palmer 17912* (G); Lexington, *Short in 1831* (NY). TENNESSEE: Lookout Mt. near Chattanooga, *Churchill in 1911* (G); Knoxville, *Ruth 753* (NY); Tullahoma, Coffee Co., *Biltmore Herb. in 1899* (US).

Some intergrades with var. *typica* may be cited: Woodside, Long Island, New York, *Ferguson 1675* (NY); Easton, Penn., *Tyler in 1896* (NY); Pricetown, Penn., *Britton in 1915* (NY); Tullahoma, Tenn., *Egbert in 1897* (NY).

6c. *Oenothera tetragona* Roth var. *velutina* (Pennell) n. comb.

*Kneiffia velutina* Pennell, Bull. Torrey Club 46: 370. 1919.

Like var. *typica*, but covered throughout with a grayish soft appressed heavy pubescence; capsules oblong, slightly clavate with incurved non-glandular hairs as well as finer gland-tipped ones.

Type locality, Garden City, Long Island, New York. Rather a distinct entity, but with fruit-shape, stature, leaf-shape, etc. of *Oe. tetragona* and seemingly different only in the abundant incurved pubescence which extends even on to the fruit. Material seen, LONG ISLAND: Garden City, *Mulford in 1902*, type (NY), *in 1897* (NY), *Bicknell in 1906* (NY); Hemp-

stead Plain, *Ferguson in 1919* (NY), *in 1918* (NY), *in 1920* (NY); Babylon, *Clute 160* (NY); Isle of Pines, *Ferguson in 1920* (NY).

6d. *Oenothera tetragona* Roth var. *Fraseri* (Pursh) n. comb.

*Oe. Fraseri* Pursh, Fl. Am. Sept. 2: 734. 1816. *Kneiffia Fraseri* Spach, Hist. Vég. Phan. 4: 375. 1835. *Oenothera fruticosa* var. *Fraseri* Hook., Bot. Mag. 6: with pl. 3545. 1837. *Oe. glauca* Michx., Fl. Bor. Am. 1: 224. 1803. *Kneiffia glauca* Spach, l.c., 374. *Oenothera fruticosa* var. *glauca* Lévl., Mon. Onoth 107. 1902.

Plant glabrous; cauline leaves mostly lance-ovate to ovate, 2–7 cm. long, 1–3 cm. wide, glaucous beneath; petals 2–3.5 cm. long; capsule-body ellipsoid-oblong, 8–12 mm. long, with stipe-like base 1–3 mm. long; seeds almost 1 mm. long, not much angled.

Type locality, "South Carolina." As the first name used in varietal rank, *Fraseri* has to be taken for this concept. Early specimens of *Fraseri* seen are as follows: "Oe. Fraseri, Hort. Paris 1828" (Ber, Del); "Oe. Fraseri, Hort. 1824, Herb. Hook." (K); "Oe. Fraseri, Lee's Garden, June 1822, Herb. Forbes-Young" (K). I have seen the type of "Oe. glauca, fol. lato-ovatis, glaucis, glaberrimis, capsule, tetrapetra tubo corolla pubescenti, Quest de Ohio, Route aux Illinois 4, Hb. Mx." (Paris). This variety ranges through the southern Appalachian Mts.; representative material, VIRGINIA: Peaks of Otter, Bedford Co., *Rydberg 9292* (NY, US); Bedford Co., *Curtis in 1871* (G, NY, P, US); Lynchburg, Campbell Co., *Britton & Vail in 1892* (NY). NORTH CAROLINA: Flat Rock, *Biltmore Herb. 673b* (NY, US); Blue Ridge, McDowell Co., *Faxon in 1872* (G); 5 mi. west of Blowing Rock, *Small & Heller in 1891* (G, NM, Paris, US); Junaluska Mt., Heywood Co., *Smith in 1882* (G, NY, US). KENTUCKY: Mts. of Ky., *Short in 1837* (BM, NY, US); Irvine, *Peter in 1834* (K); Lexington, *Short in 1837* (K). TENNESSEE: Roan Mt., *Britton in 1885* (NY); Lookout Mt., July 1929, no collector given (P).

A series of specimens at Gray Herbarium from Highlands, No. Car., made by *Harbison*, June 30, 1901, July 10, 1901, and July 13, 1901 show a complete intergradation with var. *typica*. The leaves approach *Fraseri* in shape and width, are paler below than above, but quite strigose or have some spreading hair.

6e. *Oenothera tetragona* var. *Fraseri* forma *hybrida* (Michx.) n. comb.

*Oe. hybrida* Michx., Fl. Bor. Am. 1: 225. 1803. *Kneiffia tetragona* var. *hybrida* Pennell, Bull. Torrey Club 46: 371. 1919. *K. floribunda* Spach, Hist. Vég. Phan. 4: 376. 1835, new name for *hybrida*.

Like var. *Fraseri* but with spreading hair on stems, leaf-veins, etc.

Type locality, "Hab. in Carolina superiore." Growing with var. *Fraseri* and differing from it only in pubescence. Material representative, "Caroline, *Oe. hybrida*, Herb. Michaux," type (Paris). VIRGINIA: West Hampton, Henrico Co., *Randolph & Merriman 283* (G). NORTH CAROLINA: Blowing Rock, *Robinson 139* (Ber, G); east of Blowing Rock Mt., *Heller 263* (Boiss, G, NY, P, Paris, US); Biltmore, Biltmore Herb. 669b (BM, G, US). A specimen from Eagles Nest near Waynesville, N. Car., *Standley 5428* (US) is almost glabrous and approaches *Fraseri*.

6f. *Oenothera tetragona* var. *Fraseri* forma *latifolia* (Rydb.) n. comb.

*Kneiffia latifolia* Rydb., *Torreyana* 27: 86, pl. 3. 1927.

Like var. *Fraseri*, but finely strigose.

Type locality, Craggy Mts., Buncomb Co., N. Car. Somewhat intermediate between vars. *typica* and *Fraseri*, *latifolia* seems worth recognition as a form of the latter with the broad leaves and much the same range. Representative material, PENNSYLVANIA: McCalls Ferry, York Co., *Rose & Painter 8174* (US); Ohioptyle, *Ricker 1216* (US). VIRGINIA: Mt. Elliott, *Rawlinson 138* (US); Natural Bridge, *Rawlinson 141* (US). NORTH CAROLINA: The Pinnacle, Black Mts., *Rydberg 9434* (NY, US); Eagle Cliff, Roan Mt., *Merriam in 1892* (US); Bryson City, *Hunnewell 10449* (G).

6g. *Oenothera tetragona* Roth var. *brevistipata* (Pennell) n. comb.

*Kneiffia brevistipata* Pennell, Bull. Torrey Club 46: 369. 1919. *K. semiglandulosa* Pennell, l.c.

Stem strigose; cauline leaves linear to linear-lanceolate, 2-6 cm. long, 1-5 mm. wide; petals 10-20 mm. long; ovary glabrous to glandular-puberulent, occasionally with some appressed non-glandular hairs; mature capsule-body ellipsoid to oblong, 5-8 mm. long, narrowed at base into stipe not exceeding capsule-body.

Type locality, Poplarville, Miss. This variety has puzzled me much; it is very variable and suggests *Oe. fruticosa* somewhat in capsule shape and presence of non-glandular pubescence, but it seems nearer to *Oe. tetragona* and best kept as a single entity ranging in sandy pine and oak barrens from Georgia to Louisiana and into Kentucky and Tennessee. Representative material, GEORGIA: Augusta, *Cuthbert 526* in part (NY). ALABAMA: Millerville, Clay Co., *Pollard & Maxon 178* (US); Mobile, *Mohr in 1883* (US); Gateswood, *Tracy 8497* (G, NY, US). MISSISSIPPI: Kosciusko, Attala Co., *C. A. & U. F. Weatherby 6295* (G, US); Biloxi, *Tracy 6416* (NY, US), *5064*, type semiglandulosa (NY), *Baker 1623* (NY, P); Laurel, *Tracy 3362* (NY). LOUISIANA: Opelousas, *Langlois 47* (US). TENNESSEE: Henderson, *Bain in 1892* (US). KENTUCKY: Calvert City,

Marshall Co., *Eggleston 4787* (NY); Iola, *Palmer 17909* (NY); Kuttawa, Lyon Co., *Eggleston 4656* (Del, NY).

6h. *Oenothera tetragona* Roth var. *riparia* (Nutt.) n. comb.

*Oe. riparia* Nutt., Gen. Am. 1: 247. 1818. *Kneiffia riparia* Walp., Rep. 2: 84. 1843.

Stems strigose, 7–12 dm. long; cauline leaves lanceolate, 5–12 cm. long, 5–15 mm. wide; petals 15–30 mm. long; capsule-body glandular-pubescent and with few non-glandular appressed hairs, oblong-clavate to ellipsoid-oblong, 8–12 mm. long, with stipe-like base 2–4 mm. long; seeds brown, somewhat angled, 0.8 mm. long.

Type locality, "on the banks of Cape Fear River, Wilmington, North Carolina." This variety too suggests *Oe. fruticosa* in the non-glandular hairs on the capsule, but the presence of glandular ones and the shape of the capsule relate it to *Oe. tetragona*. Representative material, NORTH CAROLINA: Wilmington, *Coville 189* (K, US), *Williamson in 1900* (NY), *Biltmore Herb. 14944* (NY, US), *Canby in 1867* (P). SOUTH CAROLINA: Santee River, *Harris C19624* (US); Blake Marsh, Charleston Co., *Alexander 53* (US).

7. *OENOTHERA PERENNIS* L., Syst. ed. 10, 998. 1758.

Perennial: stems erect or ascending, 1–6 dm. high, simple or few-branched above; basal leaf-blades oblanceolate to spatulate, 2–5 cm. long, 8–20 mm. wide, subentire to remotely denticulate, petioled; cauline leaves linear-lanceolate to oblanceolate, 2–7 cm. long, 3–10 mm. wide, entire to remotely denticulate, strigulose; uppermost reduced to linear or lance-oblong bracts; inflorescence glandular-puberulent, nodding in bud, generally more or less peduncled; hypanthium glandular-puberulent, reddish, 4–8 mm. long; sepals 5–8 mm. long, the tips sometimes somewhat free in the bud; sepals reflexed in pairs or in 4's at anthesis, glandular-puberulent; petals obcordate, 5–9 mm. long; filaments glabrous; anthers 1.5–2 mm. long; style puberulent at very base; stigma-lobes thick, 1.5–2 mm. long; capsule-body generally glandular-puberulent, ellipsoid-clavate or -oblong, 4–10 mm. long, 3–3.5 mm. wide, the narrow stipe-like base 2–4 mm. long; seeds light brown, obscurely angled, 0.6 mm. long, almost 0.5 mm. thick.

KEY TO VARIETIES

Stems strigose-puberulent. Widely distributed.

7a. var. *typica*

Stems with short spreading hairs. Rare, New Brunswick and Ontario.

7b. var. *rectipilis*

7a. *Oenothera perennis* L. var. *typica* n. nom.

*Oe. perennis* L., l.c. *Kneiffia perennis* Pennell, Bull. Torrey Club 46: 372. 1919. *Oe. pumila* L., Sp. Pl., ed. 2, 493. 1762. *Kneiffia pumila* Spach, Hist. Vég. Phan. 4: 377. 1835. *Oenothera chrysantha* Michx., Fl. Bor. Am. 1: 225. 1803.

*Kneiffia chrysantha* Spach, Nouv. Ann. Mus. Paris 4: 368. 1835. *Oenothera pumila* var. *chrysantha* Gordiner & Howe, Fl. Rensselaer Co., N. Y., 14. 1894. *Oe. gracilis* Schrad. ex Fisch. & Mey., Ind. Sem. Hort. Petrop. 2: 44. 1835. *Kneiffia Michauxii* Spach, Ann. Sci. Nat. Sér. II, 4: 167. 1835, new name for *Oe. chrysantha* & *Oe. pusilla*. *Oe. pusilla* Michx., l.c. *Oe. pumila* var. *minima* Lehm. in Hook., Fl. Bor. Am. 1: 212. 1839, new name for *pusilla*. *Kneiffia depauperata* Jennings, Journal Wash. Acad. Sci. 10: 454. 1920.

Stems strigose-puberulent to almost glabrous.

Type locality, "Canada." If we take as the type of Linnaeus' *pumila* the first reference given by that author, we find it is based on the same figure as his *perennis*, plate 188 of *Miller's Icones* (2: 188. 1757). I have seen the types of *chrysantha* and *pusilla*: "*Oe. chrysantha*, Quebec, Herb. Michaux" (Paris) and "*Oe. pusilla*, lacs Mistassins, Herb. Michaux" (Paris). Through the kindness of Professor Jennings and Dr. Graham of the Carnegie Museum of Pittsburg, I have had also the privilege of examining the type of *K. depauperata* from "lake shore, N.E. of Sioux Lookout, northwestern Ontario," *O. E. & G. K. Jennings 7501* (Carnegie). *Oe. perennis* var. *typica* ranges widely from Newfoundland to Carolina, Missouri, and Minnesota.

Representative material, NEWFOUNDLAND: Stephenville Crossing, *Mackenzie & Griscom 10357* (G, US); Bishop Falls, Exploits River, *Fernald & Wiegand 5934* (Ber, G, K, NY, US). QUEBEC: Grande-Decharge du Lac St.-Jean, *Victorin 15877* (G, NY). PRINCE EDWARD ISLAND: Rocky Point, *Fernald & St. John 7831* (G, US). NEW BRUNSWICK: St. Andrews, *Fowler in 1900* (US); mouth of Barrasois River, *Nichols 618* (G). NOVA SCOTIA: Digby, *Howe & Lang 173* (G, NY); Middleton, Annapolis Co., *Fernald, Pease & Long 22001* (G). MAINE: Ft. Fairfield, Aroostook Co., *Fernald 48* (G, K, NY, Paris, US); Orono, *Fernald in 1890* (G). NEW HAMPSHIRE: North Woodstock, Grafton Co., *Fernald 11817* (NY, US); Jaffrey, *Robinson 116* (G). VERMONT: Manchester, *Day 72* (G, US). MASSACHUSETTS: Sudbury, *Moore 925* (G); Marblehead, *Harper in 1895* (P). RHODE ISLAND: Providence, *Collins in 1892* (G). CONNECTICUT: Bridgeport, *Eames in 1894* (US). NEW YORK: Potsdam, *Phelps 714* (G, US); Richmond Valley, Staten I., *Britton in 1894* (NY, US). NEW JERSEY: Plainfield, *Tweedy in 1879* (NY, US). PENNSYLVANIA: Keating, *Metcalf in 1891* (G); mouth of the Tucquan, Lancaster Co., *Heller in 1901* (Ber, G, US). DELAWARE: Wilmington, *Commons in 1870* (US). MARYLAND: Thayerville, Garrett Co., *Tidestrom 6473* (G, US). VIRGINIA: Stribling Springs, Augusta Co., *Steele 55* (P, US); Hot Springs, Bath Co., *Hunnewell 4687* (G). NORTH CAROLINA: Biltmore, *Biltmore Herb. 1251a* (G, NY, US). WEST VIRGINIA: Morgantown, *Millsbaugh in 1890* (NY); White

Sulphur Springs, *Hunnell* 6653 (G). ONTARIO: Cedar Lake, Algonquin Park, *Macoun* 21666 (G, NY); Lake Hannah, Nipigon River, *Macoun* 803 (BM, US); Lake of the Woods, *Richardson in* 1819-22 (BM). MANITOBA: Lake Winnipeg Valley, *Bourgeau in* 1857 (Ber, G). MINNESOTA: Sandy Lake, *Sandberg in* 1891 (NY, US); Joy Cooke Park, *Rosendahl & Butlers* 4671 (G). WISCONSIN: Delavan Lake, *Skeels in* 1896 (G, NY, US). MICHIGAN: Menominee, *Shuette in* 1897 (G, K, NY, US). OHIO: Oxford, *Moseley in* 1897 (G, US). INDIANA: near Hayden, Jennings Co., *Deam* 34201 (Herb. Deam). MISSOURI: St. Louis, *Sherff* 194 (G).

7b. *OENOTHERA PERENNIS* L. var. *RECTIPILIS* Blake, *Rhodora* 25: 47, 1923.  
*Oe. pumila* var. *rectipilis* Blake, *Rhodora* 19: 110. 1917.

Stems with short spreading hairs.

Type locality, Petit Rocher, Gloucester Co., New Brunswick. Perhaps nothing more than a good form, but since its range is so restricted as compared with var. *typica*, I am letting it remain as a variety. Material seen, NEW BRUNSWICK: Petit Rocher, *Blake* 5513, type collection (Ber, G, NY, Paris, US); Bathurst, *Williams & Fernald in* 1902 (G); Miramichi, *Fowler in* 1892 (US). ONTARIO: Queenston Heights, *Macoun* 44466 in part (G, NY).

#### NAMES ABOUT WHICH I AM UNCERTAIN:

1. *Oe. fruticosa* forma *lucida* Lévl., Mon. Onoth., 108. 1902.
2. *Oe. fruticosa* var. *maculata* Lévl., l. c. 107. May be a new combination for *Kneiffia maculata* Spach, which I have listed in synonymy under *Oe. tetragona typica*, but no reference is made to that species and I cannot be certain.
3. *Oe. fruticosa* forma *sessilicarpa* Lévl., l. c. 108. A *Geyer* specimen is cited from Beardstown, Ill. and mention is made of the sessile capsules. This character and the locality would suggest *Oe. pilosella*.

#### MISCELLANEOUS NEW SPECIES

##### *Oenothera Muelleri* n. sp.

Apparently perennial, with short thick fleshy root; stems several, decumbent, 1-2 dm. long, 3-4 mm. thick, sparsely pilose; basal leaves runcinate-pinnatifid to sinuate-dentate, 8-15 cm. long, 1-1.5 cm. wide, oblanceolate, subglabrous, narrowed at wing-margined base into short petiole; cauline leaves mostly sessile, dilated at base, 3-7 cm. long, 1-2 cm. wide, oblong-lanceolate to lance-ovate in outline, dentate to sinuate-pinnatifid with lance-oblong lobes; flowers solitary in upper leaf-axils; ovary, hypanthium and sepals loosely pilose; buds nodding by the recurved hypanthium; hypanthium 14-15

cm. long, ca. 3 mm. thick except at the expanded summit, apparently with somewhat reddish longitudinal streaks without, glabrous within; sepals reflexed separately in anthesis, 3-4 cm. long, 6-8 mm. wide, lanceolate, without free tips in bud, somewhat reddish in tinge; petals probably yellow, turning rose in age, ca. 5 cm. long, 6 cm. wide, with broad shallow terminal notch having a broadly deltoid tooth 2-3 mm. long; filaments subequal, glabrous, 10-12 mm. long, somewhat dilated; anthers 12-13 mm. long; style glabrous throughout, exerted just beyond stamens; stigma-lobes linear, about 12 mm. long; capsules seen immature, subcylindric, not winged, 18-35 mm. long, ca. 4 mm. thick, pilose, prominently 4-valved at apex; seeds immature, apparently in 2 rows in each cell, 2.2 mm. long, declined, yellowish-brown, narrowly ovoid, not pitted, ridged along raphe with slight cavity and ending in a pointed tip about one-fifth of the entire length.

*Planta perennis cum radice crassa; caulibus pluribus, decumbentibus, 1-2 dm. longis, 3-4 mm. crassis, parce pilosis; foliis basalibus runcinato-pinnatifidis aut sinuato-dentatis, 8-15 cm. longis, 1-1.5 cm. latis, oblanceolatis, subglabrosis, cum petiolis brevibus; foliis caulium subsessilibus, 3-7 cm. longis, 1-2 cm. latis, oblongo-lanceolatis aut lanceo-ovatis, sinuato-dentatis aut sinuato-pinnatifidis cum lobis lanceo-oblongis; floribus in axillis foliorum superioribus solitariis; ovariis, hypanthiis, sepalisque pilosis; alabastris nutantibus cum hypanthiis recurvatis; hypanthio 14-15 cm. long, 3 mm. crasso; sepalis 3-4 cm. longis, 6-8 mm. latis, lanceolatis; petalis flavis, post florescentiam roseis, circa 5 cm. longis, 6 cm. latis, cum sinu terminale, lato et minime profundo; filamentis subaequalibus, glabris, 10-12 mm. longis; antheris 12-13 mm. longis; capsulis visis non maturis, subcylindraceutis, non alatis, 18-35 mm. longis, circa 4 mm. crassis, pilosis, cum valvis prominentibus apicalibus; seminibus 2.2 mm. longis, declinatis, anguste ovoideis.*

Type, "rare in open wood bordering the fields, and scattered in the pine savannah on Sierra Infernillo," Sierra Madre Oriental, Cieneguillas, about 15 miles southwest of Galaena, Nuevo Leon, Mexico, June 15, 1934 at 8000 ft. alt., *C. H. & M. T. Mueller no. 804*, Herbarium of Pomona College No. 210702; isotype at Gray Herbarium. The affinity of this species is uncertain. In the first place it is very difficult to be certain from the dried specimen whether the flower color is white or yellow, comparison with other species of both colors and also material from unopened buds lead me to believe that it is yellow. In which case the nearest species seems to be *Oe. macrosceles* Gray, of the subgenus *Raimannia*, from which it is amply distinct in the pinnatifid leaves and not pitted somewhat depressed seeds, as well as thicker capsule. While it superficially resembles *Oe. taraxacoides* of the subgenus *Lavauxia*, it has the narrower non-alate capsule of *Raimannia*. The actual shape of the seeds (somewhat flattened and even concavo-convex by the pressure of adjacent seeds) is more like that of *Oe. taraxacoides*.



*Oenothera Seifrizii* n. sp.

Basal part of plant missing, but would seem to be perennial, with suberect stem at least 4.5 dm. high; stem reddish, subglabrous below, villous above, rather equally leafy; lower cauline leaves subglabrous except on the ciliate margins, broadly ovate, 4-5 cm. long, 1 cm. wide, remotely denticulate, narrowed into short winged petiole; upper leaves somewhat reduced, villous on veins and margins, quite sessile; those of inflorescence becoming leafy bracts 1.5-2 cm. long; flowers not numerous, 2 or 3 in anthesis at once, the fruiting portion of the inflorescence elongating and apparently dropping its bracts, the whole villous; pedicels purplish, slender, 2-2.5 cm. long in fruit; hypanthium 13-15 mm. long, gradually enlarged upward, ca. 3 mm. broad at summit; sepals 12-13 mm. long, reflexed in pairs, villous, without any very evident free tips; petals yellow, rhomboid-obovate, 12 mm. long, 12 mm. wide; stamens subequal, filaments slender, about 5 mm. long; anthers dorsifixed, ca. 5 mm. long; style slender, retrorse-pubescent at very base, 2 mm. long; stigma-lobes 2 mm. long; capsule immature, clavate, villous, sharply 4-angled, about 2 cm. long, 4 mm. thick, 4-celled; ovules sessile, in 2 rows in each cell; seeds not seen.

Caulis 4.5 dm. longus, subroseus, infra subglabrus, supra villosus; foliis infimis caulium ciliatis, late ovatis, 4-5 cm. longis, remote denticulatis; superioribus villosis, subsessilibus; floribus non numerosis; inflorescencia villosa; pedicellis tenuibus, 2-2.5 cm. longis; hypanthio 13-15 mm. longo; sepalis 12-13 mm. longis, villosis; petalis flavis, rhomboideo-obovatis, 12 mm. longis latisque; staminibus subaequalibus; filamentis 5 mm. longis; antheris 5 mm. longis; stylo 2 cm. longo; lobis stigmatis 2 mm. longis; capsulis non maturis clavatis, villosis, angulosis, 2 cm. longis, 4 mm. crassis.

Type, Páranos of the Sierra Nevada de Santa Marta, about 30 miles inland from Dibulla, Dept. of Magdalena, Colombia at 3850 m. alt., July, 1932, *William Siefriz* 491, United States National Herbarium no. 1572285. The general aspect of this species is that of a member of the subgenus *Raimannia* with its upright elongate stems and yellow flowers, but the shape of the clavate fruit would seem to relate it to that other yellow-flowered species of the subgenus *Hartmannia*, namely *Oe. multicaulis* from which the larger flowers and upright habit easily distinguish it. So far as I can discover from the material available the sessile ovules are in two rows in each cell, whereas *Hartmannia* generally has them funicled and in more than two rows. Here we have another case of the impossibility of setting up satisfactory generic lines between these groups which I am considering as subgenera of *Oenothera*.

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# The structure and activities of myxomycete plasmodia

W. G. CAMP

(WITH TEN FIGURES)

Practically none of the descriptions and accounts of the structure and activities of myxomycete plasmodia which are to be found in the literature add anything of importance to the early observations recorded by de Bary (1859, 1864, 1887), Cienkowski (1863a, 1863b) and their contemporaries. While Micheli (1729) recognized the 'mucilaginous stage' of some of the genera of slime molds and Fries (1829) realized the importance of this stage in the life cycle of these organisms, Cienkowski was the first to observe the union of 'amoebulae' to form naked, mobile masses of protoplasm which he named plasmodia. Both Cienkowski and de Bary observed and gave a brief description of the ingestion of solid food by plasmodia and they also described the occurrence of vacuoles in the 'granular plasm' and 'hyaloplasm.' Schmitz (1879) and Strasburger (1880) established the fact that numerous nuclei are present in plasmodia.

Detailed cytological studies of the myxomycetes have dealt with changes through which plasmodia pass in becoming transformed into fructifications, the early stages of plasmodial development, and nuclear phenomena. Strasburger (1884) and Harper (1900, 1914) described spore formation by progressive cleavage; Harper and Dodge (1914) and Bisby (1914) described the process of capillitium formation in which there is a secretion or flow of extraneous, waste materials into vein-like vacuoles or invaginations traversing the protoplasm of developing fructifications; Jahn (1907, 1908) described the process of reduction division as taking place during sporophore formation, and F. A. Gilbert (1928), Wilson and Cadman (1928), Howard (1931) and H. C. Gilbert (1935) described spore germination, sexual fusion and the early stages of plasmodial development. Lister (1893) and Howard (1932) described and figured nuclear division in assimilative plasmodia and thus add materially to our knowledge of this stage.

## MATERIALS AND METHODS

Plasmodia of the myxomycete *Physarum polycephalum* were used almost exclusively in the studies upon which this paper is based, but a limited number of observations were made on plasmodia of *Fuligo septica*. The plasmodia were cultured by feeding with rolled oats according to a method developed by the writer and described in a previous paper (1936). It should be noted that this method of culturing with rolled oats as the nutrient material is not as successful with *F. septica* as it is with *P. polyceph-*

*alum.* The former does not thrive as luxuriantly as the latter under such methods of cultivation.

Permanent mounts of whole plasmodia were made by allowing them to creep over microscope slides, fixing them on the slide with absolute alcohol or Carnoy's fixative and staining with Harris' hematoxylin or Heidenhain's iron-hematoxylin. The use of albumen adhesives was found to be unnecessary. The plasmodia themselves stick to the slide quite readily when fixed as indicated. The living plasmodia were studied both with and without a microscope by examining material which had spread over the surface of moist agar plates, glass slides, and cover-slips placed over Van Tieghem cells. A Zeiss micromanipulator was used in making some examinations. Microscopical observations were made with Bausch and Lomb 10 $\times$  dry, 43 $\times$  dry, and 100 $\times$  oil immersion objectives and 6 $\times$ , 10 $\times$ , and 12.5 $\times$  oculars, that is, under magnifications ranging from 60 to 1250 diameters.

#### OBSERVATIONS AND DISCUSSION

*General features of structure and activity.* As is well known, the plasmodia of slime molds, if sufficiently supplied with water, spread over the surface of the substratum in the form of perforated sheets and anastomosing networks of vein-like branches. The advancing or anterior margin, especially in plasmodia which are moving rapidly very frequently presents an irregular or lobed appearance (fig. 1). These lobes closely resemble the advancing pseudopodia of *Amoeba proteus* and similar unicellular forms. Some portions of an advancing margin may move forward more rapidly than others and branching thus results. Two branches so formed, may grow towards each other until they touch and coalesce. It is by these processes of growth and anastomosis that a reticular structure is sometimes formed. This is the only method of reticulum development that has so far been figured and described in the literature.

In plasmodia whose advancing margin is more or less continuous or smooth except for the pseudopodial lobes mentioned above, the protoplasmic material back of the margin is very frequently distributed in a continuous sheet (fig. 2). The thickness of this sheet varies from place to place and changes constantly with the internal flowage and displacement of protoplasmic material. In general, it is thickest near the advancing margin and thinner further back. As the sheet gets thinner, due to forward motion and displacement, it becomes progressively more transparent when viewed with a microscope. The thinning-out process is by no means regular. The displacement of protoplasm is most conspicuous along stream-like or channel-like courses which are thicker and less transparent than

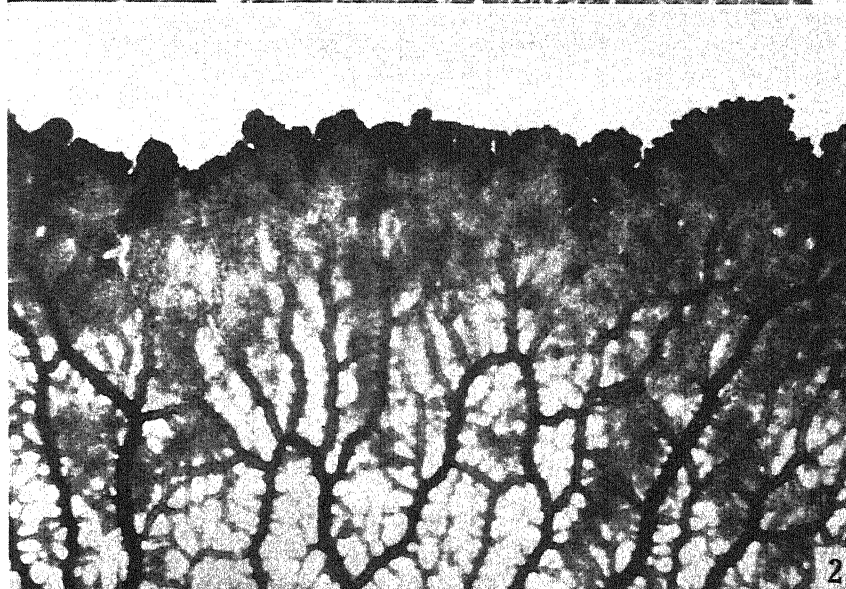
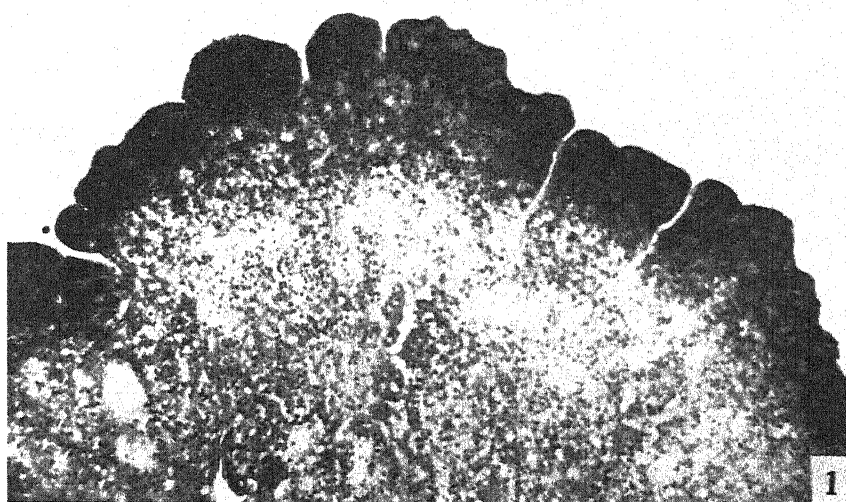


Fig. 1. Portion of the anterior margin of an advancing plasmodium showing the pseudopodial lobes.  $\times 150$ .

Fig. 2. Portion of an advancing plasmodium showing the anterior sheet and the posterior reticulum.  $\times 60$ .

adjacent portions of the sheet. It must be emphasized that these courses are not sharply defined or limited. On the contrary an impression gained from observing the movement in these channels is that the active protoplasmic streaming is more or less limited to material located in the center of the streams and the surrounding protoplasm tends to be pulled along more or less passively because of cohesion with the material of the central current. The streams in which most rapid displacement takes place, branch profusely and irregularly throughout the continuous plasmodial sheet and thus give the reticulated appearance that is so generally characteristic of plasmodia. The configuration of the net work of streams is constantly changing. A small stream may gradually widen so as to involve an increasing volume of the surrounding protoplasm, or the diameter of a stream may gradually decrease until most or all of the protoplasm in or surrounding its course has stopped moving. Sometimes a large protoplasmic inclusion may become lodged in a small channel and block it completely or change the direction of flow. In a plasmodium taken as a whole there is an almost imperceptible gradation from areas in which there is no noticeable movement, to others in which it is markedly pronounced.

The only references regarding the formation of reticula that I have been able to find in the literature, describe merely the development of such configurations through branching and anastomosis. As indicated above, the process of thinning out in a plasmodial sheet is not uniform. Irregular protoplasmic movement leads to variations in the thickness of the sheet from place to place (fig. 5). A decrease in thickness in any area of the sheet is recognized by a progressively increasing transparency. Flowage of materials away from the thinner portions of a plasmodial sheet may continue until all visibly formed bodies of the protoplasm have completely disappeared from such spots or regions. When this condition is reached, it appears that the upper and lower limiting membranes are all that remain of the continuous sheet of protoplasm and the areas present an almost perfectly hyaline appearance (figs. 3, 4). Such areas may persist for varying lengths of time without any visible changes taking place. The writer has kept them under constant observation for periods as long as twenty minutes without seeing any changes occur. That the upper and lower limiting membranes of the plasmodial sheet may persist after all visible protoplasmic materials have been displaced is indicated by the following experiments and observations. If the point of a micro-needle is inserted in a hyaline area and then withdrawn, a more or less circular region with a well defined boundary is immediately formed. Close examination of such circular areas show them to be perforations in the plasmodial membranes and their sharp boundaries constitute the fused margin of the

upper and lower surface membranes of the plasmodium. Such a perforation, made with a micro-needle, gradually increases in size. When hyaline areas with persisting membranes are left undisturbed, perforations similar to those that can be made with a micro-needle develop naturally. The

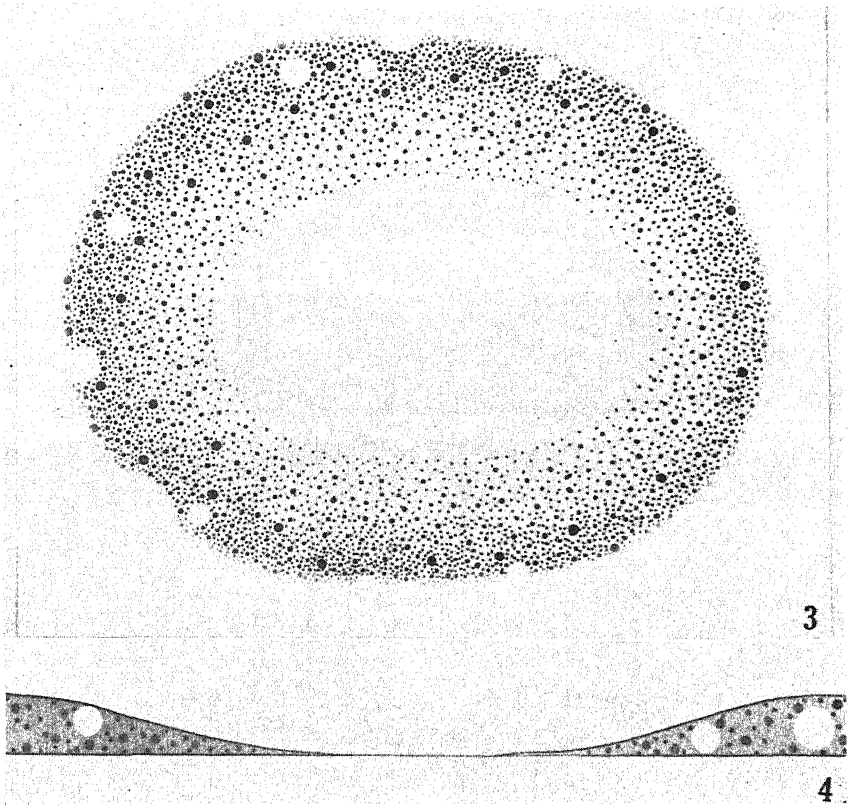


Fig. 3. Schematic drawing of a thin area of a plasmodial sheet from the center of which all visible protoplasmic materials have been displaced. Surrounding the hyaline center, where only the upper and lower limiting membranes persist, is a thin layer of homogeneous hyaloplasm. In the thicker peripheral region of the area, granules and other formed bodies are included in the hyaloplasm.

Fig. 4. The same as figure 3, shown in schematic cross section.

details of their formation is unknown, but certain observations concerning their origin can be noted. Usually they appear very suddenly and attain considerable size very rapidly. At first the margin of a perforation is irregular and exhibits a number of pointed lobes or extensions of the torn or broken membranes. This irregular, fimbriate appearance is visible for a

very brief period, and the extensions quickly retract to form an even margin. After the development of openings or perforations in a plasmodial sheet, there is a gradual and continual displacement in the protoplasm and a progressive enlargement of the openings themselves (figs. 6, 7, 8). Displacement is toward the stream-like courses referred to above. These courses eventually assume the form of a network of veins which exhibits the reticular conformation that has been so frequently described in the literature.

From the foregoing, it is seen that reticula may develop in two ways, namely, by branching at the margin of the plasmodium followed by the anastomosis of branches which happen to come into contact, and by the development of perforations in continuous plasmodial sheets followed by the displacement of protoplasm away from these perforations and into veinlike strands.

The posterior part of a plasmodium generally presents the appearance of a net-work of veins (fig. 2). With continual advance of a whole plasmodium there is displacement of protoplasm from the reticulum through the continuous plasmodial sheet and towards the advancing or anterior margin. The branches of the reticulum gradually become smaller and smaller until only extremely fine thread-like structures remain (figs. 6, 8). These thread-like branches eventually divide or break at some point and there may be immediate and fairly rapid contraction in the two free ends formed by the break, toward the larger portions of the branches where displacement of the protoplasm has not been as extensive. The contractive movement is at first quite rapid but slows down progressively and finally ceases completely. Associated with the contraction of these branches, which at first are sharply tapering and pointed, there is a very noticeable increase in the thickness of the branches themselves and with progressive shortening the ends of the branches finally become quite blunt or rounded. Displacement continues in these branches but it is always marked by a rhythmic backward and forward flow. This rhythmic flow is such that a greater amount of material is displaced in the anterior direction than in the posterior direction. As the free end of a branch gradually recedes it does not remain perfectly rounded and smooth. On the contrary, it nearly always has very delicate and tenuous projections which appear to have lagged behind as the main body of the branch moved forward (fig. 9). The size, number and arrangement of these projections changes constantly as the end of the branch moves, and each projection that is formed is slowly drawn in and disappears. When the movement of protoplasm in a branch is in a posterior direction it frequently happens that small bubble-like protrusions appear on the end of the branch. These protrusions develop

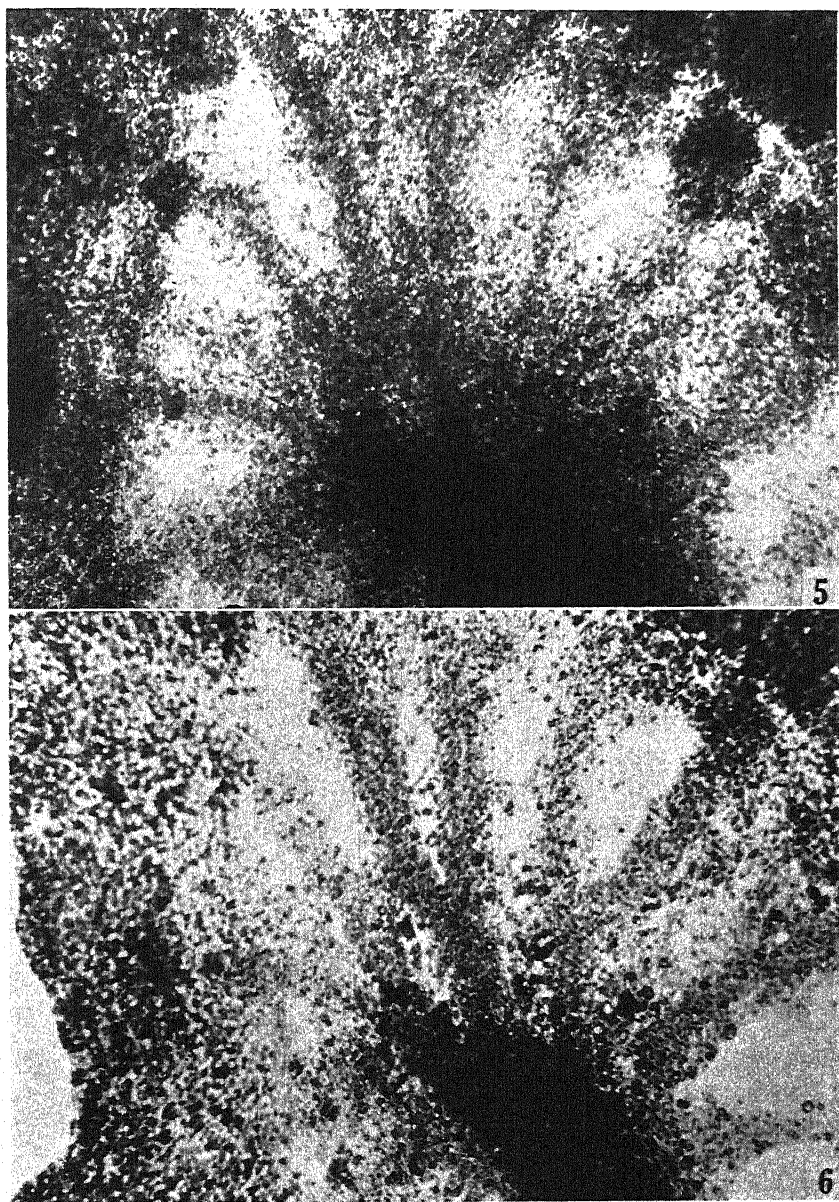


Fig. 5. Photograph showing variations in the thickness of a plasmodial sheet.  $\times 200$ .

Fig. 6. The same as in figure 5, five minutes later, showing perforations in the plasmodial sheet.



with almost eruptive suddenness. The time and way in which they develop would seem to suggest that with the increasing internal pressure due to backward displacement of protoplasm, the restraining effect of the limiting membrane which covers the end of the branch is overcome at local areas with the result that a protrusion develops at each of these areas. Another observation which may be noted here is that these protrusions always seem to develop from near the lower surface of the end of the branch.

It is not an uncommon thing to see the displacement of protoplasm in a strand of a reticulum lead to two or more constrictions. Through the formation of these constrictions followed by their breaking at some point small portions of a plasmodium are severed from the main body. These severed portions will sometimes pursue an independent course of movement and activity as small plasmodia, and the evidence at hand indicates that this is in some way correlated with their size. I have observed many times that the smallest severed portions will not move independently. The size and structural limits which will permit of this independent motion and activity are not clear.

From the time of de Bary and Cienkowski up to the present, references have been made to the layer of hyaloplasm which invests the granular plasm of plasmodia. In the most recent edition of Lister's "Monograph of Mycetozoa" (1925) the following statement is found: "The whole (plasmodium) is invested by a layer of hyaloplasm devoid of granules but merging imperceptibly into the inner granular part." Likewise in the recent volume of Macbride and Martin (1934) it is noted that "the structure of the plasmodium is not uniform; there is an outer hyaline region surrounding the inner granular portion." In the latest edition of his "Introduction to Cytology" Sharp (1934) refers to the differentiated surface layer, the ectoplasm, which "can be easily seen" and which "surrounds the granular endoplasm."

It should be noted that hyaline protrusions can frequently be seen on various parts of a plasmodium, but the surface covered by these protrusions is exceedingly small as compared to the total surface of a plasmodium. Furthermore, it appears that these hyaline protrusions are frequently not thick enough to allow the entrance or presence of formed granules and other visible structures. Not once have I been able to detect a hyaloplasmic or ectoplasmic layer which completely invests the granular plasm or endoplasm. It is recognized that an almost immeasurably thin 'plasma membrane' completely bounds the plasmodium and it is always present whether or not any special ectoplasmic or hyaloplasmic part or layer can be directly observed. Throughout the greater portion of a plasmodium



Fig. 7. The same as in figure 6, five minutes later.

Fig. 8. The same as in figure 7, five minutes later.

the protoplasmic granules of all sizes seem to lie almost immeasurably near the thin limiting surface membrane. Normally, that which might be judged to be an ectoplasmic or hyaloplasmic layer is visible only in very thin protrusions of a plasmodium or in very thin areas or margins of a plasmodial sheet or reticulum (figs. 3, 4, 10).

It is well known that many if not all myxomycete plasmodia are more or less covered with a soft slimy envelope which is not distinctly defined but is distinguishable from the marginal and surface layer. In the species which I have investigated it is most conspicuous around the thicker branches of a reticulum and is most abundant when the substratum is very moist. De Bary (1887) found that the mucilaginous material of this envelope swells in water and this property may explain its apparent abundance when the substratum is very moist. It has been a common observation that this slimy material remains adhering to the substratum from which a plasmodium has moved. The conformation of this material left behind by a moving plasmodium is the same as that shown by the plasmodium previous to its moving away and it is present in greatest abundance in those places which were occupied by the reticulum for the longest period of time. The writer has examined this slimy envelope of plasmodia by employing micro-needles and it appears that it is either extremely thin or entirely absent from the anterior margins of rapidly advancing plasmodia. The substance of this slimy envelope is in my opinion, a secretion product of the plasmodium.

*The protoplasm.* Careful microscopic examination of very thin areas of a plasmodial sheet reveals the presence of an optically homogeneous substance which has an exceedingly faint bluish gray color (fig. 3). This is the substance which is generally recognized and referred to as hyaloplasm. Scattered throughout the hyaloplasm there are numerous granules, vacuoles and particles of ingested material. The granular bodies exhibit widely varying degrees of optical differentiation and they vary in size from approximately 0.2 microns to slightly more than 1 micron. In general they are more or less spherical but some, especially the larger ones, may be irregular in shape. The smallest granules are rather highly refractive; they appear to be similar to those which Mast (1925-26) observed in *Amoeba* and designated 'alpha' granules and they are similar to the microsomes described by Chambers (1924) and which he believes to be always present in protoplasm. Many of the granules are contained in very small vesicles which bear a close resemblance to vacuoles. These vesicles do not possess well defined boundaries, and in addition to containing one or more granules they seem to be filled with a substance which is more completely hyaline and less viscous than the surrounding hyaloplasm. That the material of

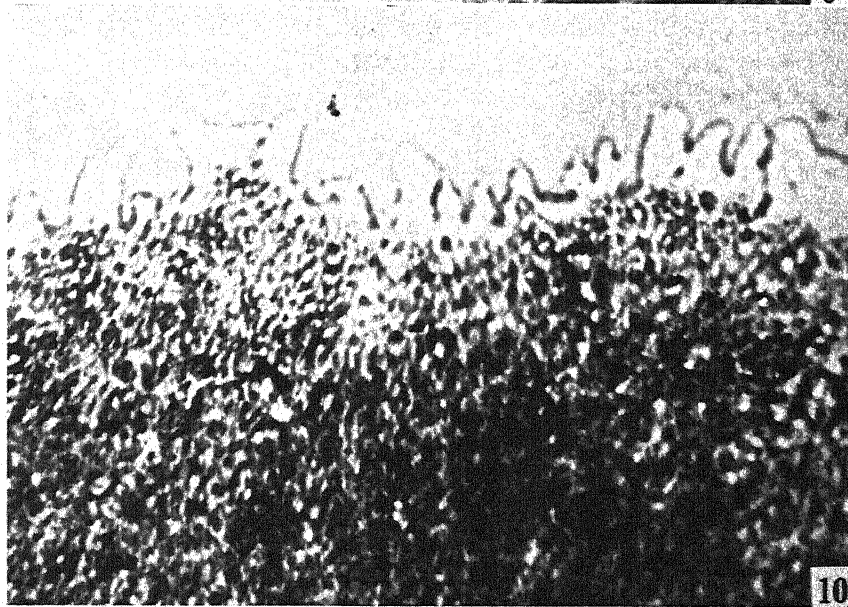
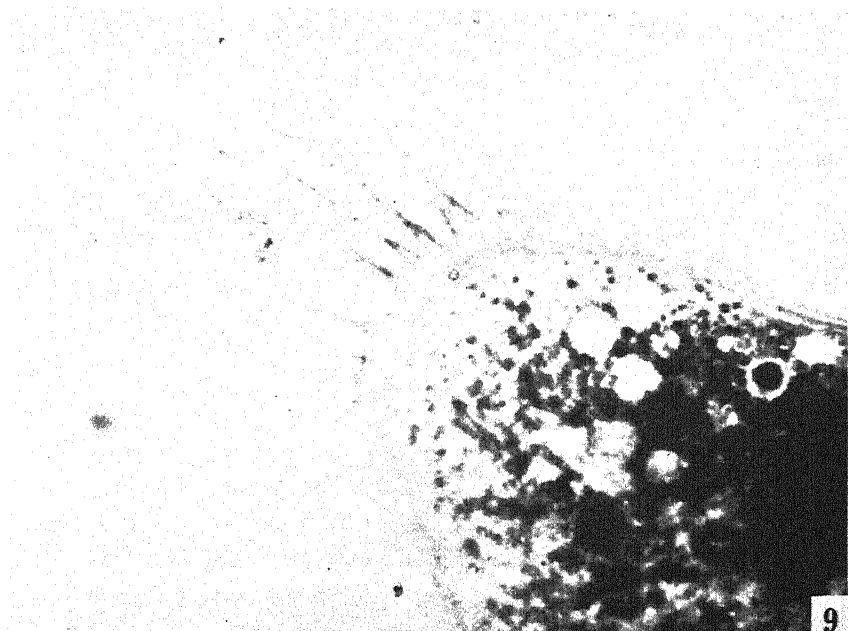


Fig. 9. Tenuous projections on the posterior end of a reticular branch.  $\times 2500$ .

Fig. 10. Hyaline protrusions of the anterior margin of an advancing plasmodium.  $\times 1000$ .

these vesicles is in a liquid state is indicated by the fact that the granules which it surrounds are always in marked Brownian movement and can very clearly be seen to move freely from place to place in the vesicles. I have observed repeatedly that granules which are not contained in hyaline vesicles as compared with those which are, may at times exhibit only very slight Brownian movement. This would seem to indicate that the surrounding hyaloplasm in the one case is more viscous than the surrounding vesicular fluid in the other case.

When, as has been indicated, the hyaloplasm and all visibly formed structures described above have, by the displacement of protoplasm, completely disappeared from the thin portions of a plasmodial sheet, the upper and lower limiting plasma membranes are all that remain of the continuous sheet of protoplasm. Surrounding these almost completely hyaline areas where only the plasma membranes persist is the very delicately defined margin of the bluish gray hyaloplasm, and at varying distances from its border occur the scattered particles and bodies previously described (figs. 3, 4). That the hyaloplasm itself may manifest fluid properties is indicated by the following observations. It has been noted that the protoplasm of slime mold plasmodia exhibits a rhythmic backwards and forwards motion. It flows first in one direction, gradually comes to a pause and then reverses its course. This rhythmic motion can be seen to occur in all parts of a plasmodium. If protoplasmic displacement is towards a hyaline area of a plasmodial sheet where only the upper and lower plasma membranes persist, there is a thickening of the sheet immediately surrounding the area. If this thickening is quite pronounced the hyaloplasm may flow out into parts of the hyaline area. When such flowage occurs the advance of the delicately outlined hyaloplasmic margin can be clearly perceived. In many observations which have been made on hyaloplasm that has been displaced in this way, I have been unable to detect optically differentiated bodies or materials at or near the hyaloplasmic margin, but such bodies are easily seen where the protoplasmic layer is apparently thicker. This indicates, it seems to me, that the hyaloplasmic sheet is not sufficiently thick to allow the presence of any of the optically differentiated particles, etc.

From time to time many biologists have felt an urge to discover some fundamental and vital unit of protoplasmic structure and in times now past consideration has been given as to whether granules or fibrils were the ultimate units of living material. It seems unnecessary to review in this paper the old ideas pertaining to this question. With the appearance of colloid chemistry as a science, protoplasm was recognized as a complex

colloid and the search for ultimate units of protoplasmic structure was gradually abandoned. The most widely accepted idea of the present time concerning the physical and chemical nature of protoplasm is that it is a polyphasic colloid system which, from microscopic examination, seems to be composed of an apparently structureless ground-substance or hyaloplasm in which occur a variety of visibly formed bodies and systems. With the growth and development of this idea there has been developing a view that vital phenomena are related to colloidal changes in the protoplasm. This view is even indicated in such studies as those of Chambers (1917) and Heilbrunn (1921, 1925) in which nuclear division was found to be correlated with phase change in the colloidal protoplasm. Included in the numerous investigations of protoplasm of recent years have been studies of its viscosity, alterations of physical state, surface tension phenomena, electrical resistance, semipermeable properties, etc. It is especially in relation to viscosity and alterations of the physical properties of protoplasm that I am here concerned.

As has been noted, microscopic examination of slime mold protoplasm shows that it is typically a concentrated suspension of visible granules and other visibly formed bodies in a more or less hyaline ground substance. Are the formed bodies suspended in a fluid medium or in a relatively viscous medium? This question has been raised many times before, not solely as regards the protoplasm of slime molds but as regards protoplasm in general. As has been pointed out by Heilbrunn (1928) some authors incline to the belief that the fundamental ground-substance or hyaloplasm of protoplasm is normally a gel of high viscosity and others hold that since protoplasm is relatively fluid the intergranular material must be fluid. It appears that in most of the viscosity studies, as reviewed by Heilbrunn, there has been an implicit if not an explicit assumption that the hyaloplasm possesses an unchanging viscosity, either relative or absolute, for a set of unchanging conditions. Such may be the case, but scant recognition is given the fact that in practically all methods which have been employed for the determination of viscosity it is impossible to establish and maintain an unchanging set of conditions. If it were possible to establish and control a set of external conditions there would still be the problem of recognizing and taking into account the internal environment of the protoplasm. From these considerations it would appear that we are a long way from making exact relative or absolute determinations of the viscosity of protoplasm.

It is manifest that any conclusions as to the viscosity of protoplasm must be based on a direct study of the living substance itself. It would seem proper to urge that a consideration of the relative viscosity of any

part or substance of a protoplasmic system be at first based on a comparison between the viscosity of that part or substance and that of some other part or substance in the same system.

If the point of a micro-needle is pressed against the surface of a plasmodium with sufficient force, the surface layer will be punctured and if the protoplasm underneath is in a liquid state it will flow out through the puncture. The resistance of the outer layer seems to vary in different places on the surface of a plasmodium and with the condition of the underlying protoplasm. If the point of a micro-needle is placed against the anterior surface of a pseudopod in which there is pronounced protoplasmic movement, it can be seen that very little pressure is required to break the surface layer. However, if the protoplasm in the pseudopod is motionless a comparatively greater degree of force may be required to produce a rupture. When a rupture is produced in such a pseudopod little or no protoplasm flows out, but a quantity of highly viscous or gelatinous protoplasm usually clings to the needle when it is withdrawn.

It has been noted that protoplasmic streaming in the branches of a plasmodial reticulum is regularly most pronounced near the center of the branch while the protoplasm near the outer surface of the branch may be motionless. The thickness of the outer motionless layer varies in different branches and its thickness changes more or less constantly. When this motionless layer is thin, punctures may be produced with little pressure, while if the layer is thick a much greater force is necessary.

Whether or not the motionless protoplasm in any part of a plasmodium is in a fluid or solid state can be determined by the application of localized pressure to that part. With the application of pressure the spacial relations of the protoplasmic constituents can be seen to change very readily if the protoplasm is fluid, but if it is solid no such change can be seen. With the application of localized pressure, such as can be made with a blunt micro-needle, to any part of a plasmodium in which the protoplasm is not moving, it can usually be seen that some of the protoplasm is fluid and some is gelatinous. The more fluid protoplasm is usually distributed throughout the gelatinous protoplasm in an intricate network of branched courses. These courses are not sharply defined or limited. On the contrary, the fluid protoplasm seems to merge or blend almost imperceptibly with the more solid protoplasm so that one can distinguish merely varying degrees of fluidity present in the protoplasm. When a needle or rod is pressed lightly against some part of a plasmodium and is then slightly agitated it can be seen that all the protoplasm for some distance around solidifies or gels completely. Without further disturbance this solid protoplasm will gradually liquefy or solate and start moving.

When a plasmodium is punctured and the fluid protoplasm flows out, as described above, the protoplasm tends to accumulate in roundish masses which cover the site of the puncture. The surface of such a mass, whether formed in air or under water, is at first quite viscid and the whole mass remains more or less fluid for a short time. Gradually, however, it loses its fluid characteristics and finally, within about two minutes becomes quite firm or solid. Dissection of a mass which has reached this condition shows that it has a rather firmly gelatinous outer rind with a highly viscous fluid center. The substance of the firm outer portion is not sharply differentiated from the internal viscous fluid, but each grades, more or less, into the other.

Masses of this kind may persist for a considerable period of time, but with periodic observations they can be seen to gradually decrease in size and finally disappear completely. The amount of time required for complete disappearance varies according to the original size of the mass. Small masses with a diameter of about one millimeter when first formed have been observed to disappear completely within two hours, while larger masses measuring six to eight millimeters in diameter have required six hours or more for complete disappearance. When these masses begin to decrease in size, examination shows that they are not as firm as when they were first formed and dissection indicates that the firm outer rind has decreased in thickness and that the highly viscous internal protoplasm has become more fluid. In fact, masses which have reached this condition can be punctured with a needle and liquid protoplasm will flow from the puncture. The thickness of the firm outer rind seems to decrease gradually until it is no more resistant than the surface of adjoining parts of the plasmodium.

When a mass of this kind is small and its various constituents can be distinguished with a microscope, it may be observed that the protoplasm contained in the mass when it is first formed is quite motionless, but movement soon starts and becomes more and more pronounced. This movement occurs first near the site of the puncture and is seen to be continuous with protoplasmic flowage in the plasmodium, but movement comes to be manifested, very gradually, in all parts of the once gelated protoplasm. The liquefaction or solation of the protoplasm is not regular but is such that a ramifying network of channels in which the protoplasm is fluid gradually develops in the gelated mass.

When plasmodia are advancing rapidly hyaline protrusions regularly appear on the anterior surfaces of the pseudopods (fig. 10). If these protrusions are punctured with a micro-needle when first formed, fluid protoplasm flows out through the opening. The indications are that the hyaloplasm contained in the tip of the protrusion flows out first and this is fol-



lowed by granular protoplasm. When protoplasmic movement in the vicinity of a hyaline protrusion stops for a short time it is much more difficult to rupture the protrusion and if it is punctured there is no outflow of fluid protoplasm. If, under these conditions, a needle is inserted into a protrusion for some distance a quantity of gelatinous protoplasm, some of which may be more or less hyaloplasmic and some granular, adheres to the needle when it is withdrawn. These observations would seem to indicate that with the cessation of protoplasmic movement in and near the hyaline protrusions, the hyaloplasm gelates and that the viscosity of the protoplasm changes with the gelation or solation of the hyaloplasm.

I have been unable to note any evidence that the change in viscosity of the protoplasm is in any way connected with a visible change in the granules and other formed bodies and substances of the protoplasm. Repeated observations were made on these bodies in portions of a plasmodial sheet during the processes of solation and gelation but I was never able to observe any visible change in them.

All of these considerations would seem to lead to the conclusion that the viscosity of the protoplasm of a plasmodium varies from place to place in the plasmodium, that it changes with changing external and internal conditions, and that alterations in the physical state, i.e., changes from sol to gel and gel to sol, take place more or less constantly throughout all parts of a plasmodium. Normally, therefore, the protoplasm of plasmodia does not have an absolute and unchanging viscosity, and variations in its viscosity seem to be due to alterations in the physical state of the hyaloplasm.

*The contractile vacuoles.* The nature of the boundaries of vacuoles has been the subject of much speculation and numerous investigations. De Vries (1885) isolated the large central vacuoles of *Allium* and *Spirogyra* by placing cells in hypertonic solutions. Chambers and Hofer (1931) performed similar experiments on onion cells utilizing a micromanipulator in addition to hypertonic solutions. They describe the vacuolar wall or tonoplast as a "highly cohesive and extensible fluid film of inappreciable thickness."

The question of whether or not contractile vacuoles have definite membranes has enlisted a great deal of attention from biologists and it is still in dispute. The existence of a morphological vacuolar membrane has been denied by Bütschli (1887), Rhumbler (1898), Taylor (1923) and others. Bütschli and Rhumbler hold that the boundary enclosing the fluid of the vacuole is a modification of the cytoplasm which does not persist but disappears with the completion of systole, while Taylor says that "the fluid of the vacuoles is enclosed within a highly viscous boundary of the endo-

plasm." More recently Day (1927) has described the vacuolar 'wall' in *Amoeba* as a "condensation membrane or gel" which disappears with each contraction.

Other investigators adduce evidence to show that a true membrane, although very delicate, actually surrounds the liquid contents of contractile vacuoles. Howland (1924) for example, employing micro-dissection methods has been able to isolate the contractile vacuoles of *Amoeba verrucosa* and *Paramecium caudatum*. By use of fixation methods Nassonov (1924) also not only claims to have demonstrated the presence of vacuolar membranes in several protozoan forms but concludes that the membranes are a part of the Golgi apparatus. From a study of serial sections and living specimens of *Paramecium*, Young (1924) came to the conclusions that "the pore, contractile vacuole and canals form a continuous, permanent ectoplasmic structure."

In my studies of the contractile vacuoles of plasmodia I have observed repeatedly that when they are very small their boundaries are not at all sharply defined but they are more or less surrounded by a layer of a substance which is optically differentiated from the hyaloplasm. This layer is by no means continuous. On the contrary it presents a broken or flocculent appearance and many of its parts appear to be connected by very delicate extensions from the parts themselves. Thus, in its distribution and arrangement it exhibits a reticular pattern. The limits or boundaries of the elements of this reticulum are not at all sharp. Instead of being clearly defined the elements of this substance seem to merge almost imperceptibly with the surrounding hyaloplasm. As a contractile vacuole gradually increases in size, the thickness of the surrounding layer of reticulated substance described above appears to gradually decrease. At the same time the boundary of the vacuole becomes more sharply defined.

In the protoplasm immediately surrounding contractile vacuoles there is an evident lack of Brownian movement of the granular particles. This fact suggests that the substance surrounding the fluid contents of the vacuoles is in the gel state. Furthermore, the way in which a vacuole collapses at systole would seem to indicate that it has a rather firm, gelatinous wall. It should be noted that there are numerous contractile vacuoles in plasmodia; they are moved about with the flowage of protoplasm but sooner or later come to lie near the surface membrane. Here they contract, presumably forcing their contents through a small opening in the membrane. Their contraction is usually quite rapid and may be uninterrupted or irregular, partial or complete. During systole the vacuole is progressively flattened in a plane which is more or less parallel to the outer surface of the plasmodium, and frequently during this process the 'wall' has an irregular

or slightly wrinkled appearance. When systole is incomplete, the small vacuolar space remaining regains a more or less spherical shape, and begins to increase in size. The phenomenon of flattening during systole would be difficult to interpret if the vacuolar boundary is assumed to be a fluid, elastic membrane. From my study of the contractile vacuoles in plasmodia, I am not inclined to believe that they are bounded by distinct morphological membranes, but my observations seem to support Day's view that the vacuolar 'wall' is a gel which disappears with each complete systole.

*Ingestion and egestion.* De Bary describes the process of ingestion by plasmodia as being "effected by definite movements; the surface of the plasmodium rises cushion-like round bodies which are in contact with it, and the margins of the raised part gradually run together over them and cover them." This description gives only a partial picture of the process. The process described above can be seen to occur when the bodies to be ingested are fairly large or are adhering to the substratum, and it seems to be, in fact, a preparatory maneuver on the part of the plasmodium, preliminary to the actual process of ingestion. If very small pieces of food such as particles of finely pulverized rolled oats are scattered on a slide over which a plasmodium is creeping, the process of ingestion itself may be observed. When the plasmodium comes in contact with the food particle, the latter tends to be pushed forward, away from the plasmodial margin. However, that part of the plasmodium directly behind the food ceases its forward movement while, as de Bary describes, on either side and above and below, the protoplasm flows out for a slight distance and tends to surround the food particle. The food particle thus comes to lie very close to the concave surface of the plasmodial membrane, and sooner or later the particle rapidly sinks quite deeply into the margin of the plasmodium. A flask-shaped depression with the food particle contained in its bulbous part is thus produced. The neck of this flask-shaped depression constricts very rapidly until it is completely closed and for a brief period of time there persists a thread-like structure connecting the boundary of the newly formed vacuole with the plasma membrane of the plasmodium. This thread-like structure eventually breaks at some point and that portion of it which is attached to the plasma membrane is drawn outward, while the part which is attached to the vacuolar boundary is drawn inward, both disappearing almost immediately. These observations indicate that a portion of the plasma membrane of a plasmodium comes to surround the food vacuoles when they are formed. This method of ingestion has been described by Grosse-Allerman (1909) as it occurs in *Amoeba terricola* and has been called 'invagination.'

It is well known that the plasmodia of slime molds deposit a conspicu-

ous amount of discharged refuse matter on surfaces over which they have passed. In the species which I have cultured by feeding with rolled oats there is a considerable quantity of egested starch grains in such debris. These grains and other solid particles are arranged in a pattern that conforms more or less with that previously exhibited by the plasmodium before creeping away, the places which were occupied by the branches of a plasmodial reticulum being marked by a double line of discharged particles.

It should be noted that with the ingestion of solid particles in the manner previously described, a quantity of water is also taken into the food vacuoles when they are first formed. It appears that the amount of water in the vacuoles gradually diminishes until the solid particles are very closely surrounded by the protoplasm. Egestion of solid particles can be seen to take place when they come to lie very near the surface of the plasmodium. The details of the process of egestion have been difficult to observe but apparently it is marked by the breaking of the thin retaining surface layer of protoplasm and frequently by the forceful ejection of the particle which is being egested. When the surface layer of protoplasm breaks there is an immediate and very rapid contraction and drawing in of the edges about the break. This contraction is frequently accompanied by a very rapid outward displacement of protoplasm which lies directly underneath the particle which is being egested and this action is such that the ejected body is thrown some distance. It appears that in the process of egestion the vacuolar membrane comes to be continuous with the surface membrane of the plasmodium.

The phenomena relating to ingestion and egestion seem to indicate that the boundaries of the food vacuoles are somewhat different from those of the contractile vacuoles and that the former are limited by membranes which are, in all respects, similar to the plasma membrane of the plasmodium. The fact that contractile vacuoles coalesce and fuse quite readily while food vacuoles have never been seen to do so would also seem to indicate a difference in their 'walls.'

*Protoplasmic movement.* The phenomena of protoplasmic streaming and amoeboid movement have long attracted the attention of biologists and attempts to explain them have varied with the changing conceptions of the physical nature of protoplasm. Berthold (1886) sets forth the view that protoplasmic streaming in vegetable cells has its cause in local alterations of the surface tension between the fluid protoplasm and the cell sap. Bütschli's (1894) observations and experiments upon "oil-foams" and investigations of protoplasmic structure and activities led him to accept Berthold's view and apply it to all forms of amoeboid movement. Rhumbler (1898) from his studies of movement in rhizopods interprets pseudopod

formation as a result of surface tension phenomena. The surface tension theory demands that the surface of the protoplasm shall be in a liquid state and that the whole protoplasmic mass shall obey the laws of fluids. Calkins (1933) notes that "with the more modern conception of protoplasm as a colloidal aggregate in the physical state of an emulsion in which the external and internal protoplasm of *Amoeba* are in the relation of gel and sol, the difficulty of applying the laws of fluids became apparent and the hypothesis based upon surface tension has been generally abandoned." It should be noted that Rhumbler himself (1910, 1914) eventually changed his views and came to regard amoeboid movement as due to alterations in the colloidal state of the protoplasm, involving solation and expansion at the anterior end and gelation and contraction at the posterior end. Rhumbler's later view has been extended and perfected by Hyman (1917). Employing the potassium cyanide test for metabolic gradients which was developed by Child (1915), Hyman claims to have demonstrated that the extreme tip of the advancing pseudopod of *Amoeba* is the most actively metabolic part. According to her an amoeba moves in the following way: "The ectoplasm is an elastic tensile gel which exerts a tension upon the more fluid endoplasm. At some local spot in this gel, a chemical change occurs, an increase in metabolic rate or an alteration of some kind of metabolism. As a result of this, substances or ions are set free or removed which alter the colloidal state of the ectoplasm, and cause it to become more liquid, that is, to go over into the sol state. At the region where the liquefaction has occurred, the protoplasm must necessarily flow out owing to the tension exerted by the ectoplasm. As soon, however, as the pseudopodium extends out into the water, its surface gelatinizes." She finds support for her belief that liquefaction results from the production of ions in the work of Bancroft (1913) and Clowes (1916) who demonstrated phase reversibility in diphasic physical systems with electrolytes. Hyman admits being "unable to explain how the amoeba alters its own metabolic processes, or how it is determined where the local liquefaction in the ectoplasm is to occur."

Another and more recent explanation of amoeboid movement has been offered by Mast. According to Mast (1926) the body of an amoeba is divided into four rather distinct parts: (1) the plasmasol which is a central, fluid, elongated region, (2) the plasmagel which is a solid layer in the form of a closed sac completely surrounding the plasmasol, (3) the plasmalemma a very thin elastic surface layer or membrane, and, (4) a hyaline layer between the plasmagel and the plasmalemma, most prominent at the anterior ends of active pseudopods where it forms a hyaline cap. Mast (1931) describes the mechanics of locomotion in *Amoeba* as follows: "There are four

primary processes involved in locomotion in *Amoeba*; attachment to the substratum, gelation of the plasmasol at the anterior end, solation of the plasmagel at the posterior end and contraction of the plasmagel at the posterior end.

"Ordinary gelation of the plasmasol at the anterior end extends the plasmagel tube forward as rapidly as it is broken down at the posterior end by solation.

"Contraction of the plasmagel tube at the posterior end, drives the plasmasol forward.

"An amoeba is a turgid system, owing to this the plasmagel is continuously under tension. The plasmagel is elastic and consequently is pushed out at the region where its elastic strength is lowest. This results in the formation of pseudopods."

Mast's view would seem to demand that during locomotion the plasmalemma slide freely over all parts of the plasmagel but adhere to the substratum. He affirms all of this except to say that the plasmalemma adheres to the plasmagel on the lower side of the organism while it is drawn forward on the upper surface over the plasmagel. On this point his view is rather difficult to understand.

With reference to what causes gelation at the anterior end and solation at the posterior end in moving amoeba, Mast is on the whole uncertain. He cites the work of Edwards (1921) in which it was demonstrated that acids tend to produce gelation and alkalies, solation, and in his own experiments (1931, 1932) demonstrates that both pressure and light may cause gelation.

The phenomenon of protoplasmic streaming and locomotion in plasmodia have been given very little attention, except that it has been a common observation that there is a rhythmic backward and forward flow of the protoplasm in which the forward streaming is of somewhat longer duration than the backward. It is not my purpose at this point to attempt an explanation of the movement of plasmodia, but merely to discuss some observations and views which have a bearing on the subject. Protoplasmic movement or locomotion in a plasmodium is so similar to the same phenomenon in the rhizopods that when the correct explanation is found for the one, it will probably hold true in most of its aspects for the other, and, as several authors have suggested this explanation may give in addition, a key to the understanding of the movement of flagella, cilia, and even muscular contraction.

It has been noted that the anterior margins of plasmodia are frequently divided into pseudopodial lobes filled with granular protoplasm. These pseudopods in turn, may have anterior protrusions which are more or less

hyaline (fig. 10). The size, shape and position of these protrusions vary considerably and change more or less continuously. At times they appear as caps which extend completely across the face of the pseudopods, but very often their width is less than that, and more than one may be present on a single pseudopod. The way in which these protrusions develop is strikingly similar to the way in which the bubble-like protrusions develop at the free ends of posterior reticulating branches. They frequently form with almost eruptive speed, and always seem to originate near the lower surface of the lobe. The way in which they develop seems to indicate that there is a weakening of the limiting membrane at local areas resulting in an overcoming of the restraining effect of the surface membrane by internal pressure. These active protrusions have the faint bluish gray color characteristic of hyaloplasm. When they are first formed, only very few granules or optically differentiated substances may be visible near their tips, although at their basal ends the protoplasm contains numerous granules, vacuoles and other inclusions. Very rarely have I been able to distinguish a distinct line of demarcation between the granular protoplasm at the base and the hyaloplasm at the tip. In all cases where such a line seems to exist, it appears that the protrusions are not large enough to permit the entrance of inclusions. In fact, the way in which these protrusions develop, seems to indicate that in the early stages of their formation, their size, generally, is insufficient to allow the entrance of granules, etc., along with the liquid hyaloplasm. As they enlarge, however, their diameter increases and gradually more and more inclusions are carried forward. Thus, in many newly formed protrusions, there is a graded distribution of granules and other optically differentiated parts of the protoplasm, between their tips and bases. Occasionally protrusions appear which, throughout their whole period of development are filled with granular protoplasm, but such protrusions are always noticeably larger than those which are more or less hyaline. After hyaline protrusions are fully formed, the granular protoplasm contained in their basal portions gradually mixes with the hyaloplasm in their tips, and sooner or later the protrusions present the appearance of mature lobes in which there is a more or less uniform distribution of protoplasmic inclusions. The development of both lateral and apical protrusions on these small lobes, may in turn lead to a change in their size and shape.

An actively advancing plasmodium as seen from the side, has a very thin anterior edge. Behind this edge there is a rather sharp, upward inclination of the upper surface of the plasmodium leading to a ridge which may be 200 or more microns above the surface of the substratum. Posterior to this ridge the plasmodium is seen to be progressively thinner towards

the free ends of the reticular branches. This shape is similar to that of advancing amoebae as figured by Jennings (1906), in that the anterior edge is very thin. It should be noted that Mast takes no account of this structural feature of advancing amoebae. I have indicated above that this feature is in agreement with the hyaline appearance of protrusions at the anterior margin of plasmodia, by noting that the thickness of these protrusions when they are first formed is such that the granules and other formed bodies of the protoplasm do not enter them. As they increase in thickness granules and other bodies enter and mix freely with the hyaloplasm. Before any visible structures enter one of these protrusions there may be a fairly sharp line of demarcation between the hyaloplasm which it contains and the granular plasm posterior to it. The appearance which results from such a condition seems to be similar to the appearance of the tips of advancing pseudopods of *Amoeba* as described by Mast. Mast's interpretation of this condition is that a hyaline fluid filters through a thin layer of the plasmagel to form a hyaline cap underneath the anterior tip of the plasmalemma. From my observations on plasmodia I have found no evidence at all that a gelled layer separates the hyaloplasm of the anterior protrusion from the granular plasm of the main body of the pseudopod. Anterior protrusions of considerable thickness are from the first filled with granular protoplasm and this seems to support the view that hyaline protrusions are not thick enough to permit the entrance of granules, vacuoles, etc., along with the hyaloplasm.

In an early paper Mast (1924) expresses the opinion that the protoplasm of the hyaline cap of advancing pseudopods of *Amoeba* is a gel but in a later paper (1926) he inclines to the view that the substance contained in these caps is fluid. Mast's explanation of amoeboid motion would seem to demand that during the active forward extension of a pseudopod, the substance in the hyaline caps shall be fluid. However, at the time of a brief pause in the forward extension of a pseudopod this substance may gelate and it seems that this is what happens in the hyaline pseudopodial protrusions of plasmodia. It has been noted that if a pseudopodial protrusion is punctured while it is forming, fluid protoplasm will flow from the opening, but if protoplasmic movement ceases in and near the protrusion, it is rather difficult to puncture it and when a break is made in the surface there is no outflow of protoplasm. This view seems to support and extend Hyman's opinion that some degree of gelation in pseudopodial extensions immediately follows their formation.

Hyman describes pseudopods of *Amoeba* as advancing by "little lunges." Whether or not eruptive stages in the advance of pseudopods is a common feature in locomotion among the rhizopods is unknown to the



writer, but observations on *Vahlkampffia* show it to be pronouncedly characteristic of this amoeboid form. Reference has been made to the eruptive way in which protrusions appear on the anterior face of the pseudopods of plasmodia and at the posterior ends of reticular branches and it has been suggested that this kind of sudden and rapid out-thrusting is due to internal pressure following a localized diminution of the restraining effect of the limiting surface layer. This view seems to be in harmony with that of Hyman and demands that the plasmodium shall be a turgid system in which the outer part is continuously under tension. That an active plasmodium is such a system is indicated by the fact that puncturing of a plasmodium may be followed by a pronounced outflow of fluid protoplasm. It has been noted that the outer part of a plasmodium seems to be in a more or less gelated condition and this gelated layer corresponds in general with the plasmagel of *Amoeba* as described by Mast. It appears that in a turgid plasmodial system it is this gelated layer which is continuously under tension, and that its shape and distribution expresses in general the conformation of the whole plasmodium. It is very thin at the tip of extending pseudopods and at the posterior ends of reticular branches and its thickness varies greatly elsewhere in different parts of the plasmodium. It should be pointed out that the protoplasm in parts of a plasmodium may be inactive although not gelated in any marked degree. It has been indicated that whether or not the protoplasm in a region is gelated can be determined by the application of localized pressure. With the application of such pressure there is a visible change in the spatial relationships between the formed bodies of fluid protoplasm, while in gelated protoplasm no such change occurs. The composition of gelated protoplasm in a plasmodium does not seem to be different from the more fluid protoplasm. The same types of granules and other formed bodies can be seen in both and the main difference between them seems to be merely a matter of degree of fluidity.

Mast (1926) describes "masses of plasmagel of various sizes and shapes" which are "frequently seen floating free in the plasmasol." This is not a common phenomenon in plasmodia but it occurs to the extent that masses of granular plasm in regions of close reticulation may be dragged this way or that by rapid streams adjacent to and even surrounding them. There seems to be no sharp differentiation between the fluid and gelated protoplasm of plasmodia, one merging more or less into the other. This condition is particularly evident in masses which have been formed by the outflow of fluid protoplasm from a puncture in any part of a plasmodium. Gelation in these masses takes place a few minutes after their formation and appears to be more pronounced in their outer parts.

The size, shape and location of the channel-like courses through which

protoplasmic streaming takes place seems to be determined in large degree by the abundance and distribution of the formed bodies of the protoplasm, ingested inclusions, etc. It has been noted that in thin plasmodial sheets, streaming seems to take place more readily in those places where, apparently through chance distribution, the protoplasmic inclusions of all kinds are of a comparatively small size. Furthermore, it has been observed that large inclusions may come to be lodged in a channel insufficient in size to allow their passage. In such cases the protoplasmic stream may be deflected around the particle in one or more directions or streaming at that place may stop entirely. The lodging of a single inclusion in the way described with the consequent deflection of the stream in two or more directions frequently constitutes the first step in a more or less continuous series of changes whereby other inclusions come to be lodged at the same place so as to form a kind of island around which the streaming protoplasm is continuously deflected. Along the sides of large channels in a plasmodial sheet there is very often a noticeable accumulation of large inclusions which have apparently simply settled out of the flowing protoplasm. All of these processes which I have just described show marked analogies to the process of silting as it occurs in the sediment-laden waters of rivers in the course of their meanderings and changing velocities.

#### SUMMARY AND CONCLUSIONS

1. Plasmodial reticula develop in two ways, namely, by branching followed by the anastomosis of branches which happen to come into contact, and by the development of perforations in continuous plasmodial sheets followed by the displacement of protoplasm away from the perforations into vein-like strands.

2. The protoplasm of myxomycete plasmodia is composed of an apparently structureless ground-substance or hyaloplasm in which occur a variety of granules, vacuoles and other visibly formed bodies.

3. The viscosity of the protoplasm varies in different parts of a plasmodium and is influenced by variations in external and internal conditions. Viscosity changes may be attributed to alterations in the physical state of the apparently structureless hyaloplasm.

4. Contrary to numerous statements in the literature, I find no thick hyaloplasmic layer which completely invests the granular plasmodium. An almost immeasurably thin plasma membrane encloses the plasmodium and the protoplasmic granules and formed bodies of all kinds may lie very near this membrane. That which is generally judged to be an ectoplasmic or hyaloplasmic layer occurs only in very thin protrusions of a plasmodium or in very thin areas or margins of a plasmodial sheet or reticulum.

5. The outer part of the protoplasm of a plasmodium is generally in a

gel condition. The thickness of this gelated layer varies in different parts of a plasmodium but is usually very thin at the tip of extending pseudopods and at the posterior ends of reticular branches. There is no sharp differentiation between the gelated and the fluid protoplasm, one merging imperceptibly with the other.

6. The protoplasm immediately surrounding contractile vacuoles is in the gel state and the boundaries of these vacuoles are thought to be different from those of food vacuoles. The way in which contractile vacuoles discharge their liquid contents differs from the manner in which food vacuoles perform a similar function at the time of egestion.

7. Plasmodia ingest solid particles by invagination, a method which has been described as occurring in certain amoebae. The food vacuoles are surrounded by a membrane which is probably similar to the plasma membrane of the plasmodium. At the time of egestion of undigested particles from the food vacuole, its membrane becomes continuous with the plasma membrane.

8. Protoplasmic movement and locomotion in plasmodia are similar to the same phenomena in the rhizopods and to streaming in tissue cells. Pseudopod formation takes place along the advancing anterior margin. In actively moving plasmodia very thin protrusions which may or may not be hyaline are continuously developing on the anterior faces of the pseudopods and it is through the development of these protrusions that they gradually extend forward. These protrusions seem to be produced by internal pressure following a local diminution of the restraining effect of the limiting surface layer. The fluid protoplasm of plasmodia tends to show rhythmic backward and forward flow and the formation of pseudopodial protrusions is more or less synchronized with the forward displacement of the protoplasm. Thin protrusions similar to those which develop on the anterior pseudopods frequently appear on the posterior ends of reticular branches, their formation being more or less synchronized with the backward flow or displacement of protoplasm. The visible hyaloplasmic parts of a plasmodium are merely not thick enough to permit the entrance of granules and other formed bodies. A plasmodium is a turgid system in which the outer gelated layer when present and the plasma membrane are under continuous tension. The size, shape and location of channel-like courses along which protoplasmic streaming takes place are continually limited and oriented to some extent by the character and distribution of the formed bodies of the protoplasm.

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# INDEX TO AMERICAN BOTANICAL LITERATURE 1933-1937

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## The effect of phosphorus on chromosome and nuclear volume in a violet species<sup>1</sup>

W. P. PIERCE

(WITH PLATE 8)

In a recent paper (1936) the author pointed out graphically that the distribution of chromosome size and volume was not constant from cell to cell in the same individuals of several native species of violets. In an attempt to analyze more carefully factors responsible for such variation in chromosome size, a study of the effects of phosphorus has been attempted, because of the importance of this element in the formation of the nucleo-proteins and nucleic acid. The present study has been limited to *V. conspersa* Reichb., a species which had previously been studied when growing under normal conditions.

### HISTORICAL

As Lutman points out (1934), "the effect of a deficiency or of a super-abundance of one or more of the inorganic elements of plant food on the size and growth of plants has been recognized since the earliest days of plant physiology." However, as might be expected, most of the data of this sort have to do with the gross effect on the plant body, such as yield, root versus top development, tendency to early or late flowering, and the like.

The prime importance of the element phosphorus in the formation of nucleo-proteins, nucleic acid, and lecithin, which are present in nearly every living cell, has been pointed out by Loew (1891, 1903) and others. The literature pertaining to the general effects of phosphorus on the plant body as a whole has been quite thoroughly reviewed by Lutman (1934).

In general it may be said from a survey of some of the literature that, although phosphorus seems to have a decided effect in increasing crop yield, root growth is stimulated most, and, in some cases at least top growth is retarded. Brenchley (1929) found that the element is apparently of special importance in the formation of barley roots during their early development. Yet Tueva (1929) found that barley roots would absorb enough phosphorus in the first five weeks to carry the plant to normal development. The delicate violet seedling, owing to its initial slower growth, would probably require a longer period of time to store an adequate amount of phosphorus.

<sup>1</sup> Published with the approval of the Director of the Vermont Agricultural Experiment Station.

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However, the literature on the direct effect of an element on the size of cells, nuclei, and particularly of chromosomes seems to be scanty. Bamford (1931) in his cytological study of corn and wheat seedlings showed the destructive effect of a calcium deficiency on cell structure. With the exception of Lutman's paper (1934), the present writer has been unable to obtain citations dealing directly with this specific effect of phosphorus.

Lutman (1934) has studied the effects of an excess or absence of nitrogen, phosphorus, potassium, magnesium, or calcium in the culture solution upon cells of Japanese millet, rape, buckwheat, and garden beet. A deficiency in any one of these elements induced a premature vacuolization of root tip cells. Epidermal cells (including guard cells) and their nuclei were smaller if phosphorus, nitrogen, or potassium was absent. On the other hand an excess of nitrogen induced the formation of unusually large epidermal cells; while in the case of phosphorus this effect was noticeable only with buckwheat and beet.

#### MATERIAL AND METHODS

The plants used in this experiment were seedlings of *V. conspersa* Reichb., approximately two weeks old, sister seedlings from the same clone, which had germinated later than usual in a flat out of doors. When transplanted the seedlings were about 2 to 2½ cm. in total length, still in the cotyledonary stage, with but a few secondary rootlets developed.

The method of sand culture was used for two reasons. (1) Most investigators have found that sand cultures produce a considerably better root growth than water cultures (McCall (1916), Stolhane (1914), *et al.*). (2) The sand culture furnished a medium more nearly comparable to soil, probably giving better aeration to the root system, a critical factor in the growth of young violet seedlings. A pure silica sand was used, after it had been washed in distilled water. The containers consisted of waxed cardboard, with small holes in the bottom to prevent soil saturation.

Seven seedlings were planted in each container, and two weeks later the number was thinned down to the five strongest individuals. Four culture solutions were used as follows:

#### *Solution I (complete nutrient)—modified from Tottingham (1914)*

Sol. A:	KNO <sub>3</sub>	1.7 gm.
	KH <sub>2</sub> PO <sub>4</sub>	7.0 gm.
	MgSO <sub>4</sub> ·7H <sub>2</sub> O	10.0 gm.
	Dist. water	500.0 cc.
Sol. B:	Ca(NO <sub>3</sub> ) <sub>2</sub>	12.0 gm.
	Dist. water	500.0 cc.

#### *Solution II (lacking in phosphorus)—modified from Walster (1920)*

Sol. A:	KNO <sub>3</sub>	1.7 gm.
	KCl	4.5 gm.

	MgSO <sub>4</sub>	10.0 gm.
	Dist. water	500.0 cc.
Sol. B:	Ca(NO <sub>3</sub> ) <sub>2</sub>	12.0 gm.
	Dist. water	500.0 cc.

*Solution III (excess phosphorus)—Lutman (1934)*

Sol. A:	KNO <sub>3</sub>	1.7 gm.
	KH <sub>2</sub> PO <sub>4</sub>	7.2 gm.
	MgSO <sub>4</sub>	10.0 gm.
	Dist. water	334.0 cc.
Sol. B:	Na <sub>2</sub> HPO <sub>4</sub> · 12H <sub>2</sub> O	17.5 gm.
	Dist. water	334.0 cc.
Sol. C:	CaH <sub>2</sub> (PO <sub>4</sub> ) <sub>2</sub> · H <sub>2</sub> O	7.0 gm.
	Ca(NO <sub>3</sub> ) <sub>2</sub>	12.0 gm.
	Dist. water	334.0 cc.

In the case of each of these solutions, just previous to using, they were diluted 100 times with distilled water.

*IV. Tap water.*

The experiment was run over a period of slightly more than two months, the water content of the pots being kept as near the optimum as possible. Some root tips were fixed at the end of the first month after planting, but the majority of the tips were harvested at the end of the second month.

Two fixing fluids were used, (1) Flemming's medium fixative, and (2) Allen and Wilson's modification of Bouin's solution. Although root tips from both solutions were cut and examined, all measurements were finally made from those fixed in Flemming's medium. Sections were cut eight microns thick and stained in Heidenhain's iron-alum-haematoxylin. The method used in making chromosome measurements has been fully discussed in the writer's previous paper (1936). Briefly, it consisted in the use of a pliable paper rule marked off in millimeters, this being applied to the magnified drawings. As previously mentioned, all chromosomes measured were drawn with a camera lucida from carefully selected metaphase plates, at a projected magnification of 3100 diameters, with the aid of a Zeiss 2 mm. apochromatic objective and a 20× compensating ocular. The source of illumination was an improved Zeiss lamp, transmitted through a prism reflector.

OBSERVATIONS AND DATA

The measurements of chromosome lengths and nuclear diameters were all taken from a comparable region of mature root tips, or more specifically the most active region of the periblem and dermatogen of the root tip (Pierce, 1936). Although most of the data consist of chromosome measurements, a table of the frequency distribution of nuclear diameters is also included.

1. *Chromosome measurements.*—Two distinct methods of analysis of the data secured from the measurement of chromosomes found in root tips grown in the different culture solutions are presented. (1) The variation in *total* chromosome length from cell to cell in each solution used. (2) The *distribution* of individual chromosome lengths, considered from the more quantitative method of grouping all the chromosomes measured in the case of each culture solution.

As previously pointed out (Pierce, 1936), the recorded figures for individual chromosome length are probably less in most cases than the actual existing chromosome length, due to the occurrence of slight vertical curvatures in the chromosomes which could not be measured by this method. Because of this fact, and also because of the liable error involved in any method of measuring such small objects, the figures presented cannot be considered as absolutely correct. It does seem, however, that, in view of the relatively large differences found to occur in chromosome length and volume, the figures may be considered significant.

In table 1, the total chromosome length for each cell and the average chromosome width are recorded separately. A study of this table shows, also, that the total lengths recorded are arranged in descending order, from shortest to longest, to bring out at a glance the resulting range in variation occurring with the use of each solution. Finally, in the last column is presented the computed volume<sup>2</sup> of the set of chromosomes which most nearly approached the median total length for each culture solution. It is to be noted that the starred figures (plates no. 9, 10, 11, 12) in the minus phosphorus group are greater than the rest. This was apparently due to the fact that these chromosomes were from root tips that were fixed at the end of the first month, and as might be expected they were less affected than the rest.

The frequency polygons in figure 1 present the frequency distribution of the individual chromosome lengths, found under the different cultural conditions of growth. The number measured in each case, 240, was considered sufficiently large to be significant if plotted in this type of curve. An examination of the polygons will show that with the possible exception of one polygon, minus phosphorus (fig. 1), the profiles tend to show a fairly close approach to the normal curve of distribution. The irregularity of the minus phosphorus curve will be explained in the discussion.

To facilitate an analysis of the data presented in the four polygons, the weighted mean chromosome lengths, the modal class, as well as the total range in size for each curve are presented in tabular form. Perhaps

<sup>2</sup> The formula used in computing the volume of the diploid chromosome complements was  $\pi r^2 l$ , where  $l$  = the sum of the individual chromosome lengths in the complement.

TABLE 1

*Differences between the total lengths and the average widths of the diploid chromosome sets under the different cultural conditions*

	CHROMOSOME PLATE	TOTAL LENGTH	AVERAGE WIDTH	COMPUTED VOLUME
Complete Solution	1	37.9 $\mu$	.45 $\mu$	4.75 cu. $\mu$
	2	38.6 $\mu$	.45 $\mu$	
	3	41.6 $\mu$	.45 $\mu$	
	4	42.2 $\mu$	.42 $\mu$	
	5	43.2 $\mu$	.45 $\mu$	
	6	43.2 $\mu$	.38 $\mu$	
	7 <sup>*</sup>	44.6 $\mu$	.42 $\mu$	
	8	46.2 $\mu$	.42 $\mu$	
	9	46.8 $\mu$	.45 $\mu$	
	10	47.7 $\mu$	.45 $\mu$	
	11	48.5 $\mu$	.48 $\mu$	
	12	49.0 $\mu$	.42 $\mu$	
Excess Phosphorus	1	44.5 $\mu$	.38 $\mu$	7.39 cu. $\mu$
	2	45.0 $\mu$	.45 $\mu$	
	3	46.1 $\mu$	.42 $\mu$	
	4	46.2 $\mu$	.42 $\mu$	
	5	48.5 $\mu$	.48 $\mu$	
	6	49.0 $\mu$	.42 $\mu$	
	7	49.3 $\mu$	.45 $\mu$	
	8	50.8 $\mu$	.45 $\mu$	
	9	51.1 $\mu$	.48 $\mu$	
	10	51.6 $\mu$	.48 $\mu$	
	11	53.1 $\mu$	.48 $\mu$	
	12	54.5 $\mu$	.48 $\mu$	
Minus Phosphorus	1	24.3 $\mu$	.32 $\mu$	2.41 cu. $\mu$
	2	25.6 $\mu$	.32 $\mu$	
	3	26.1 $\mu$	.32 $\mu$	
	4	27.6 $\mu$	.32 $\mu$	
	5	31.1 $\mu$	.32 $\mu$	
	6	31.4 $\mu$	.29 $\mu$	
	7	33.7 $\mu$	.24 $\mu$	
	8	37.2 $\mu$	.29 $\mu$	
	9	*37.5 $\mu$	.32 $\mu$	
	10	*38.5 $\mu$	.32 $\mu$	
	11	*41.1 $\mu$	.38 $\mu$	
	12	*46.6 $\mu$	.32 $\mu$	
Tap Water	1	27.9 $\mu$	.25 $\mu$	1.92 cu. $\mu$
	2	31.6 $\mu$	.25 $\mu$	
	3	31.6 $\mu$	.29 $\mu$	
	4	32.7 $\mu$	.29 $\mu$	
	5	32.7 $\mu$	.25 $\mu$	
	6	32.7 $\mu$	.29 $\mu$	
	7	33.1 $\mu$	.25 $\mu$	
	8	33.7 $\mu$	.29 $\mu$	
	9	33.7 $\mu$	.29 $\mu$	
	10	34.2 $\mu$	.29 $\mu$	
	11	39.5 $\mu$	.29 $\mu$	
	12	40.0 $\mu$	.25 $\mu$	

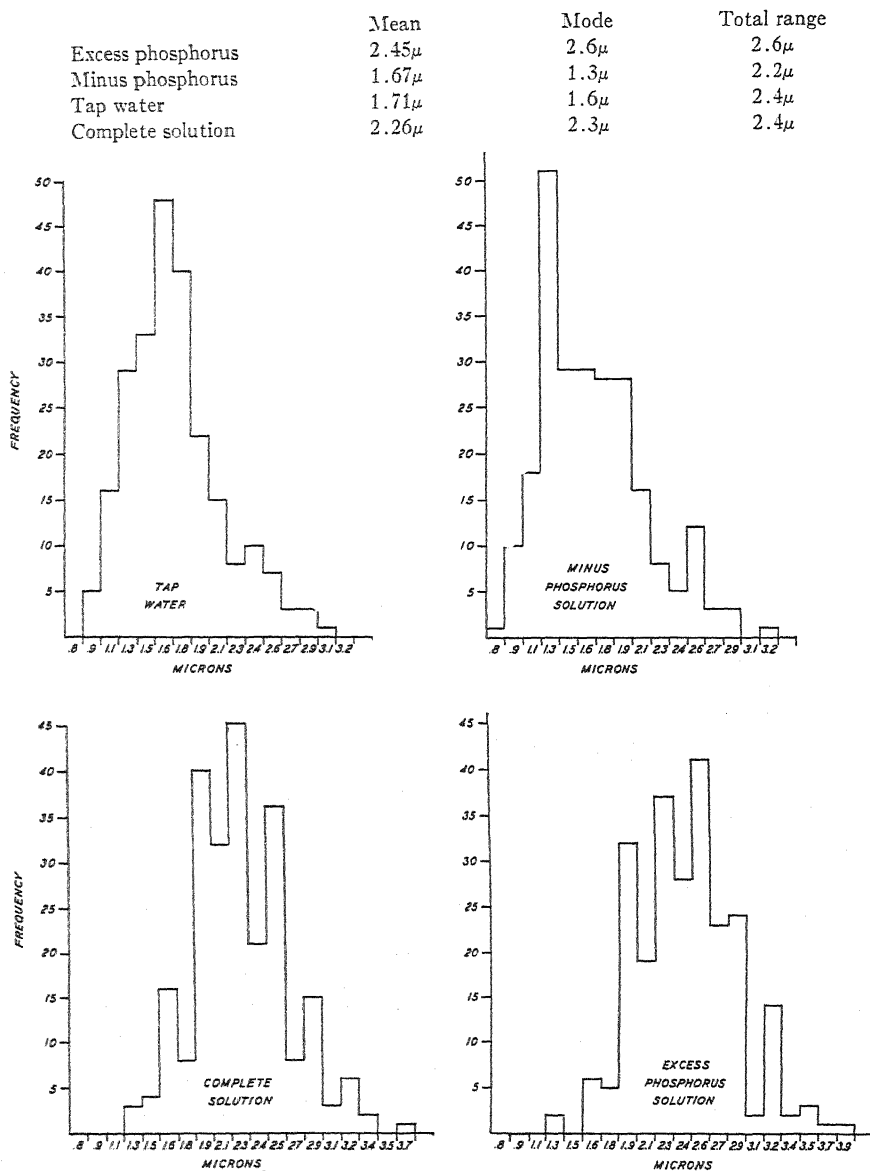


Fig. 1

the most striking change apparent from these figures is the downward shift in the modal class of chromosome size in the complete nutrient solution from  $2.3\mu$  to  $1.3\mu$  in the case of the minus phosphorus and to  $1.6\mu$  in the case of tap water. There is also to be noted a slight upward shift to

2.6 $\mu$  in the modal length of the chromosomes grown in an excess phosphorus solution. The mean chromosome lengths computed show approximately the same general trend.

The figures denoting the range, or difference, in chromosome length from the shortest to the longest measured show a surprisingly slight variation. It may be inferred from the figures that the chromosome length shifts *en bloc*, or throughout the diploid complement as a whole, rather than in just a few chromosome individuals, or even the majority. In other words it is apparently not only a shifting of the peak of the curve alone but rather of the whole profile.

II. *Nuclear measurements.*—The table of measurements presented below shows the frequency of distribution of the nuclear diameters of fifty

TABLE 2

*Nuclear measurements from cells of the dermatogen and periblem showing the frequency of distribution of diameters in microns*

SOLUTION	FREQUENCY									
	4.4	4.9	5.5	6.0	6.6	7.1	7.7	8.2	8.8	9.3 microns
Complete Solution				2	11	13	19	3	2	
Excess Phosphorus					3	6	16	19	5	1
Minus Phosphorus	5	12	22	10	1					
Tap Water	1	9	25	10	5					

*Computed mean diameters:* complete solution=7.3 $\mu$ ; excess phosphorus=7.8 $\mu$ ; minus phosphorus=5.3 $\mu$ ; tap water=5.5 $\mu$ .

nuclei taken in each case from that region of the root tip from which the chromosome drawings were made. Due to the rather small range of size in the diameters measured, this number of measurements was considered to be fairly representative. As in the case of the individual chromosome lengths, the weighted mean diameter was computed for each series. It is apparent that these mean nuclear diameters do not vary much from the modal class.

#### DISCUSSION

From the foregoing data presented in graphical and tabular form it appears not unlikely that an excess or a deficiency of the element phosphorus affects chromatin mass to a considerable extent, whether measured by nuclear or chromosome volume. The rather marked differences in chromosome length and width is also apparent in the equatorial plate stages shown in the plate.

A comparison of the figures given in table 1, denoting the volume of the set of chromosomes which in each case most nearly approached the median, discloses the following facts. The volume of those chromosomes

grown in root tips watered with a solution containing an excess of phosphorus is nearly twice that of those grown in a nutrient solution, and three times that of those grown in root tips deprived of phosphorus. The rather marked reduction of chromosome volume found in root tips grown in tap water is probably due to an insufficient quantity not only of phosphorus but of all the nutrient elements.

The unsymmetrical nature of the minus phosphorus polygon can best be explained by the interesting, though perhaps not unexpected fact that the effect of phosphorus starvation seemed to be cumulative, and considerably greater at the end of two months than at the end of one. In other words, there was included in the polygon the measurements of four diploid sets of chromosomes, eighty which were considerably longer than the

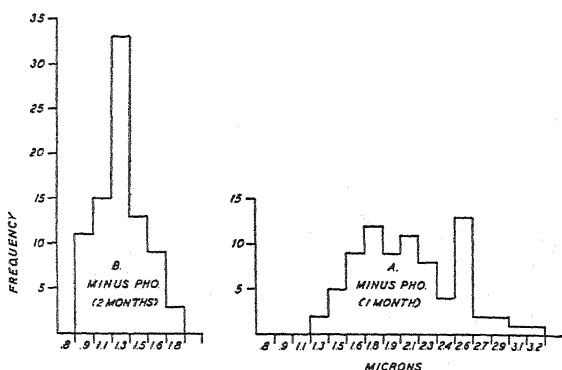


Fig. 2

majority. This is shown rather clearly in the distribution curves shown in figure 2, in which the distribution of lengths of the eighty chromosomes mentioned above is compared with the lengths of eighty chromosomes drawn from root tips which had been subjected to phosphorus starvation for two months instead of one. The marked shift of the modal class, as well as the extremes, to a smaller size in curve B is at once apparent. It seems significant also that the polygon B is a normal type curve, with the peak coinciding with the peak in the larger curve (fig. 1). As was mentioned above, the same cumulative effect is shown in the figures of total chromosome length in table 1.

Lutman (1934) has said that "the effects of a lack or excess of a given plant inorganic nutrient can be seen as readily in the plant as a whole as in the cells or organs which compose it, but it reveals itself soon even in very young organs." This observation has been substantiated somewhat

in the present experiment. Plants grown in a minus phosphorus solution and tap water showed the greatest gross effect, being decidedly poor in both top and root growth. Although no measurements of cell size in the root tips were made, the cells appeared noticeably smaller and nuclear divisions were very difficult to find. This would indicate in the root at least, that the smaller size was due to both cell size and cell number. The excess phosphorus plants showed a slightly more vigorous growth, and appeared to have slightly larger cells, but the difference appeared to be so slight in comparison with the plants grown in the nutrient solution, that the difference is not considered significant.

In view of the fact that Lutman found nitrogen to affect nuclear size in the root tips of several genera of plants, it would seem probable that nitrogen, and perhaps other elements as well, would affect chromosome size in somewhat the same manner as phosphorus does.

Some of the conflicting points of view in regard to the relative importance of the number and size of chromosomes, in its relation to organ form and organ size in plants and animals, are discussed in the writer's previous paper. Recently Watkins (1936) found "that the average length of the bivalent chromosomes of *Yucca aloifolia*, a small tree 2-3 meters high, is approximately 1.3 times that of the bivalents of *Y. louisianensis*, an acaulescent species," thus suggesting a tendency to a parallelism between the chromosome length and the size of the adult plant.

The data presented in the present experiment would seem to indicate that from a genetical point of view a rather marked change in chromosome size does not necessarily result in a corresponding change in morphological expression but rather in a dwarfing effect on the whole plant. A further extension of such a course of investigation as the one reported in the present study might have an important bearing upon the direct relationship between cell, nuclear, and chromatin volume and the "gigas" and "nana" phenomena found in plants.

This study was suggested by Professor B. F. Lutman and carried on under his stimulating direction and advice. To Professor A. Gershoy I am indebted both for the use of his pedigreed stock, as well as his friendly criticism. In addition I wish to express my gratitude to Professor G. P. Burns for criticism of the manuscript.

#### SUMMARY

Nuclear and chromosome measurements in plants of *Viola conspersa* show considerable differences when the plants are grown in nutrient solutions lacking or containing different amounts of phosphorus. Chromosome volume in root tips watered with a solution containing an excess of phos-



phorus is nearly twice that of those grown in a complete nutrient solution, and three times that of those grown in root tips deprived of phosphorus. The cumulative effect of phosphorus starvation on chromosome length and volume is discussed.

Chromosome volume of plants grown in tap water shows an even greater reduction than in those plants grown in a solution lacking phosphorus.

The relation of these findings to the size and vigor of the plant as a whole is discussed.

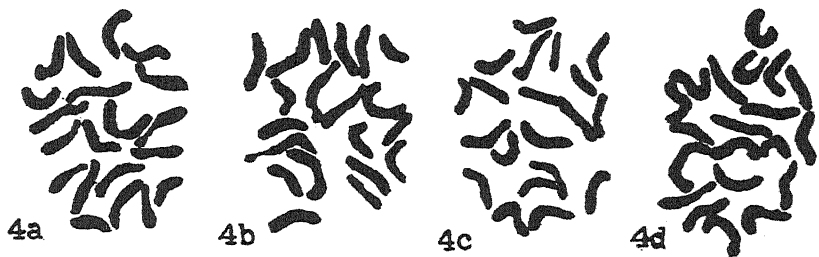
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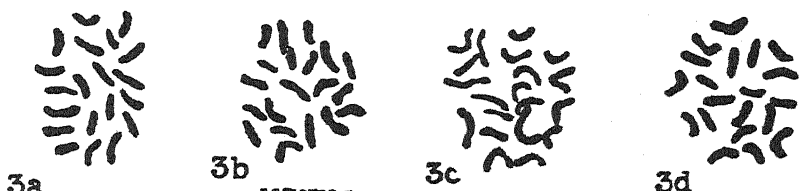
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#### Explanation of plate 8

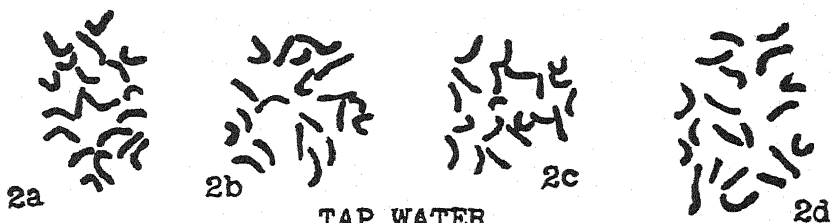
The figures shown are selected metaphase plates drawn with the aid of a camera lucida, at a projected magnification of 3100 diameters. All but two of those shown were drawn from cells of the perilem, the two exceptions (figures 4a and 1d) were from cells of the dermatogen.



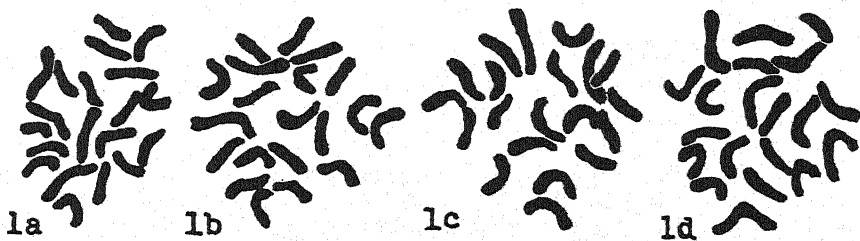
EXCESS PHOSPHORUS



MINUS PHOSPHORUS



TAP WATER



COMPLETE SOLUTION



## Studies in *Penstemon* IV. The section *Ericopsis*

DAVID D. KECK

Previous papers in this series, treating the sections *Saccanthera*, *Hesperothamnus* and *Cryptostemon*, have appeared in the University of California Publications in Botany 16: 367–426. 1932; Madroño 3: 200–219. 1936; and *ibid.* 3: 248–250. 1936, respectively.

The collections in the following herbaria have been studied for the present paper, and I wish to thank the curators of each for making these materials available to me.

A—Arnold Arboretum, Harvard University, Jamaica Plain, Mass.

BYU—Brigham Young University, Provo, Utah.

C—University of California, Berkeley.

CAS—California Academy of Sciences, San Francisco.

CI—Carnegie Institution of Washington, Stanford University, Calif.

CM—Carnegie Museum, Pittsburgh, Pa.

F—Field Museum, Chicago.

GH—Gray Herbarium, Harvard University.

M—Missouri Botanical Garden, St. Louis.

Minn—University of Minnesota, Minneapolis.

ND—University of Notre Dame, Notre Dame, Ind.

NY—New York Botanical Garden.

Ph—Academy of Natural Sciences, Philadelphia.

Po—Pomona College, Claremont, Calif.

RM—Rocky Mountain Herbarium, University of Wyoming, Laramie.

SU—Dudley Herbarium, Stanford University, Calif.

UARiz—University of Arizona, Tucson.

US—United States National Herbarium, Washington, D. C.

Utah—Utah State Agricultural College, Logan.

I have examined approximately 950 sheets in my study of this section, but for purposes of brevity it has been necessary to curtail their citation considerably in the case of the better known units.

### AFFINITIES OF THE SECTION ERICOPSIS

New species in this primarily West American genus have been made known so rapidly in recent years that classification of the subdivisions of the genus, terms necessary for the convenient discussion of the forty or more subgroups, has lagged. Tentative classification of these generic subdivisions indicates that *Penstemon* contains about six obvious subgenera, the largest of which **Eupenstemon**, comb. nov. (as a section, Benth. in DC. Prodr. 10:327, 1846), is divisible into at least a dozen defensible sec-

tions. *Ericopsis* is a new name proposed for one of these and its eleven species are the basis of this paper.

Three subsections are of use in circumscribing the natural species-groups, which, in this case, may each be on the order of a cenospecies. The *Caespitosi* with seven species, the *Linarioides* with three species, and the *Laricifolii* with one species are here proposed as subsections. Together they have characters in common that seem to emphasize their natural relationship and there is no obvious transition into any other section.

It is hazardous to guess in just what order the three subsections are linked together, but it can be safely stated that the closest obvious affinity is apparent between the *Caespitosi* and the *Linarioides*.

Through *P. retrorsus* there is a close similarity with *P. Moffatii* Eastw., *P. pumilus* Nutt. and *P. dolius* Jones, of the "Cristati," which is very suggestive of a direct relationship, and I am inclined to name that section, which has such manifold relationships, as the forerunner of the section *Ericopsis*.

*Penstemon ambiguus* Torr. has a salverform corolla and so distinctively oblique a corolla-limb that it has been thought to be one of the most unique species in the genus. Very closely related to it, however, is *P. Thurberi* Torr., which conforms much more closely to the usual form of corolla found in *Penstemon*. The two are grouped as the "Ambigui" and their relationships appear to be with section *Ericopsis*, possibly through the subsection *Laricifolii*. *Penstemon laricifolius* and the "Ambigui" have in common glabrous herbage, linear or filiform leaves, and corollas externally glabrous. In addition, I have observed in the field that the white corollas of *P. laricifolius* subsp. *exilifolius* reflect the same glistening sheen from their lobes that is found in *P. ambiguus*. I have not observed this elsewhere in the genus although it may occur in other white-flowered species.

#### *Ericopsis* Keck, sect. nov.

Plants low, generally tufted at base, often repent, with a  $\pm$  suffrutescent caudex; leaves entire, crowded, filiform to broadly linear, when wider, less than 3 cm long, thickish, rarely with evident midnerve; inflorescence a narrow leafy racemiform thyrus; corolla tubular, slightly to definitely ampliate, obviously bilabiate, the base of the lower lip bearded with yellowish hairs; anther-cells ovate to oblong, less than 1 mm long, widely divaricate, dehiscent throughout and across the broad line of contact; staminode linear, not dilated apically, prominently bearded dorsally. Species occurring for the most part with sagebrush, juniper and pinyon, on high plateaus and mountains of Southwestern United States and Baja California. Type species, *Penstemon laricifolius* Hook. et Arn. The name *Ericopsis* means "like Erica" and refers to the heather-like appearance of the foliage in the majority of the species.

## KEY TO THE SUBSECTIONS

Inflorescence, including the outside of the corolla, glandular-pubescent; stems pubescent; leaves linear to linear-oblongate, if broader, very short.

Caespitose, the caudex  $\pm$  repent, forming mats; corolla nearly tubular, or somewhat expanding, rarely with guide-lines in throat, the throat 2-ridged within, forming a low palate, the upper lip erect. . . . . 1. *Caespitosi*

Stems ascending to erect from a non-repent caudex; corolla not plicate within throat, the upper lip spreading. . . . . 2. *Linarioides*

Inflorescence, including the outside of the corolla, glabrous; stems essentially glabrous; leaves filiform. . . . . 3. *Laricifolii*

Subsection 1. *Caespitosi*, new subsection

Usually extensively repent, forming mats up to 2 m across; caudex usually slender; stems rarely more than 1-2 dm tall, pubescent; leaves linear or broader; corolla externally viscid, slightly ampliate, the throat somewhat expanding dorsally, with 2 ventral ridges within, the upper lip erect or nearly so, usually slightly exceeded by the spreading lower lip.

## KEY TO THE SPECIES OF CAESPITOSI

A. Leaves puberulent to canescent (often very sparingly in *P. caespitosus* subsp. *suffruticosus*); calyx-lobes not prominently scarious-margined.

Pubescence of leaves not closely appressed but spreading.

Leaves oblanceolate, the larger 20-30 mm long, 3.5-4.5 mm wide, coarsely retrorse-pubescent, not mucronate; calyx-lobes lance-oblong, united  $\frac{1}{4}$ - $\frac{2}{3}$  their length. . . . . 1. *P. retrorsus*

Leaves linear, more crowded, the larger to 12 mm long, to 1.5 mm wide, finely cinereous-puberulent, sharply mucronate; calyx-lobes linear, free almost to base. . . . . 2. *P. leucroides*

Pubescence of leaves appressed; leaves mucronate.

Plants little spreading; leaves cinereous-whitened, oblanceolate to spatulate-oblong or obovate; herbage of inflorescence very obscurely viscid; corolla 4-5 mm broad at throat. . . . . 3. *P. Thompsoniae*

Plants widely spreading; leaves greenish, linear to oblanceolate or spatulate, but smaller; herbage of inflorescence more obviously viscid; corolla 3-4 mm broad at throat (wider in subsp. *desertipecti*). . . . . 4. *P. caespitosus*

AA. Leaves glabrate at least apically (except in *P. Crandallii* subsp. *atratus*); calyx-lobes usually prominently scarious-margined (except in *P. acaulis*).

Stems essentially none; flowers borne in the basal rosette of foliage; leaves scabro-glutinous, not mucronate. . . . . 5. *P. acaulis*

Stems elongated; leaves not scabro-glutinous, mucronate.

Corolla with guide lines within throat; leaves 12-30 mm long, linear to oblanceolate or spatulate. Southwestern Colorado and adjacent borders. . . . . 6. *P. Crandallii*

Corolla without guide lines; leaves mostly 10 mm. long, linear. Central Utah. . . . . 7. *P. abietinus*

1. *PENSTEMON RETRORSUS* Payson ex Pennell

*Penstemon retrorsus* Payson ex Pennell, Contr. U. S. Nat. Herb. 20: 373. 1920.

Stems ascending-erect, 10-20 cm tall, loosely tufted, from suffrutescent short rootstocks; leaves broadly oblanceolate (or the upper linear-oblanco-

late), moderately crowded, retrorsely pubescent on both faces, the hairs not closely appressed, the larger leaves 2–3 cm long, 3.5–4.5 mm wide; inflorescence not crowded or densely leafy; calyx-lobes lance-oblong, acuminate, united  $\frac{1}{3}$ – $\frac{2}{3}$  their length, very slightly scarious-margined, densely cinereous-pubescent, moderately glandular; corolla 16–20 mm long, up to 5 mm wide when presed, nearly tubular, probably deep blue-purple; anther-sacs ovate, 0.6 mm long; staminode orange-yellow bearded nearly throughout, but most strongly at apex.

Valley of Uncompaghre River, Montrose County, Colorado. "Collected on a dry adobe hill near Montrose, Colorado, altitude 1,740 meters, in flower, June 15, 1915, by Edwin Payson (no. 673)."

COLORADO. Montrose Co.: Montrose, *Payson* 673 (NY, type; isotype RM), *Dawson* (NY).

This species remains very little known and is apparently a closely restricted endemic. It is well-marked. There is a surprising resemblance between it and *P. Moffatii* Eastw., of the group *Cristati*, which is found in the same county. This similarity is sufficiently arresting to warrant speculation as to whether or not *P. retrorsus* may not have arisen through hybridization between such species as *P. Moffatii* and *P. Crandallii* or their progenitors. Morphological and distributional factors suggest the possibility strongly, and cytological investigation of the three species might prove very enlightening.

Within the present section, the closest connections are with *P. Crandallii* subsp. *atratus*, the quality of the pubescence and the habit being the principal differences between them.

## 2. *PENSTEMON TEUCRIOIDES* Greene

*Penstemon teucrioides* Greene, Pl. Baker. 3: 23. 1901.

Stems ascending or erect, from a stout horizontal woody rootstock, 4–10 cm tall; herbage densely cinereous-puberulent throughout; leaves linear, involute, sharply mucronate, 5–10 or 12 mm long, crowded; calyx lobes almost wholly herbaceous, nearly linear, viscid-puberulent, ca. 5 mm long; corolla pale blue to blue-purple, 15–19 mm long; anther-sacs ovate, small; staminode golden bearded throughout.

Common in Gunnison Valley of west-central Colorado, at elevations of 2,200 to 3,350 m. "Collected at Sapinero, 19 June [1901]; said to be common there, on dry ground, [C. F. Baker] no. 186."

COLORADO. Chaffee-Gunnison counties: Monarch Pass, *Porter* 2041 (CI, Ph). Gunnison Co.: Gunnison, *Shear* 3858 (NY, US); Sapinero, *Baker* 186 (ND, type; isotypes C, CI, GH, M, NY, Po, RM, SU, US); between Cebolla and Lake City (CAS). Saguache Co.: Sargents, *Pennell* 6302

(F, GH, M, NY, RM, US). Hinsdale Co.: Lake City, *Purpus* 721, in part (F).

### 3. *PENSTEMON THOMPSONIAE* (Gray) Rydb.

*Penstemon pumilus* var. *Thompsoniae* Gray, Syn. Fl. 2 (1): 269. 1878.

*P. Thompsoniae* Rydb., Bull. Torr. Club 36: 690. 1909.

Stems prostrate or ascending, arising from a woody caudex surmounting a fibrous rooted underground stem, scarcely creeping, forming tufts or mats; leaves thick, spatulate-oblong to obovate, tapering to a petiolate base, obtuse or rounded at apex, mucronate, cinereous-whitened with a closely appressed puberulence; sepals acuminate to attenuate, with or without a narrow scarious margin toward base, scarcely to moderately viscid; corolla 12–18 mm long, the throat somewhat ampliate; anther-sacs ovate-oblong; staminode golden bearded nearly throughout, but most strongly at apex.

#### KEY TO SUBSPECIES

- A. Stems tufted, crowded; inflorescence compact, prominently leafy; corolla nearly tubular, slightly ampliate, 13–18 mm long. . . . . 3a. *P. T.* subsp. *typicus*
- AA. Stems few, remote; inflorescence more open, the flowers not partially concealed by the leaves; corolla tubular-campanulate, 12–14 mm long. . . . . 3b. *P. T.* subsp. *Jaegeri*

#### 3a. *Penstemon Thompsoniae* subsp. *typicus* Keck, nom. nov.

*Penstemon pumilus* var. *Thompsoniae* Gray, l.c.

*P. pumilus* var. *incanus* Gray, l.c. The type, collected in the Pahrnagat Mts., Nevada, by Searls, is a tiny scrap. Better material from near the type locality places this small-leaved form definitely within *P. Thompsoniae* subsp. *typicus* through a succession of intermediate forms that defy the maintenance of this as a distinct entity.

*P. Thompsoniae* Rydb., l.c.

*P. incanus* Tidestrom, Contr. U. S. Nat. Herb. 25: 495. 1925.

Caudex merely suffrutescent; leaves oblanceolate to spatulate-oblong, acuminate to the petiolate base, usually obtuse, but the lower sometimes rounded apically.

Southern Utah, northern Arizona, and southeastern Nevada, on rocky or gravelly slopes of the Upper Sonoran Zone, at 1,500 to 2,200 m elevation. "S. Utah, *Mrs. Thompson*."

UTAH. "S. Utah," 1873, *Bishop* (GH); "S.W. Utah," *Siler* (GH, cited as *P. pumilus* var. *incanus*). Garfield Co.: Bryce Canyon, *Stanton* 1019 (Ph). Kane Co.: Kanab, 1872, *Mrs. Thompson* (GH, type); Navajo Well, *Jones* (Po). ARIZONA. Mohave Co.: Beaver Creek, *Purpus* 8295 (C, M, US); Mokiak Pass, *Palmer* 380 (GH, M, NY, Ph, US); rim of Burnt Canyon, *Cottam et al.* 4186 (BYU, Ph); Wild Cat, *Cottam et al.* 4116 (BYU, Ph); Peach Springs, *Eastwood* 18683 (CAS, CI); Truxton Springs, *Lemmon* 4151 (GH); between Hackberry and Peach Springs (A, Po); Hackberry,



*Jones 4658* (A, C, CAS, CI, F, NY, Ph, Po, RM, SU, UAriz, Utah); Kingman-Yucca road, *Braem* (SU). Coconino Co.: Cosnino, *Rusby* (F, M, NY, Ph, US). Yavapai Co. (?): between Ash Fork and Peach Springs, *McKelvey 2169* (A). Navajo Co.: S. of Winslow, *Peebles 9530* (US). NEVADA. White Pine Co.: Connor's Pass, 25 mi. E. of Ely, *Keck 628* (C, CAS, CI, GH, NY, Ph, SU, US). Lincoln Co.: Pahrnagat Mts., 1871, *Searls* (GH, type of *P. pumilus* var. *incanus*); Mt. Irish, *Purpus 6329* (C, US, a dwarf form very similar to the last); Pioche, *Jones* (Po), *Minthorn 81* (C).

3b. *Penstemon Thompsoniae* subsp. *Jaegeri* Keck, subsp. nov.

Caudex saepe suffruticosissimus, caulibus patulis paucis, foliis dealbatis laminis ellipticis obovatisve abrupte ad petiolam reductis, inflorescentia elongata laxa foliolosa, corolla modice ampliata 12-14 mm longa 4-5 mm lata.

Confined to the mountain ranges of Clark County, Nevada.

Type: *Edmund C. Jaeger* (Pomona College Herbarium, no. 159547), collected in the Trout Creek area, 2,750 meters (9,000 ft.) elevation, Charleston Mts., Clark County, Nevada, June 27, 1926; isotype CAS, labelled "on cow-trail from Trout Creek to crest." Another sheet from the same area is labelled, "Plentiful on west slope near Trout Creek, alt. 9,500 ft." and was collected on the same day, *Jaeger* (Po). These three sheets bear the notation "flowers deep purple." An additional collection of this subspecies was made on Potosi Mountain, Clark Co., June 28, 1930, by *Jaeger* (Po).

The various specimens of subsp. *Jaegeri* are very similar and appear to represent a distinct ecotype of the species that has possibly been selected by climatic agencies of those higher elevations at which it is found.

*Penstemon Thompsoniae* appears to have a natural basis notwithstanding the several indistinct races that compose it and in spite of its very close affinity for *P. caespitosus*. There is scarcely a morphological, or in fact a geographical, gap separating *P. Thompsoniae* subsp. *typicus* from *P. caespitosus* subsp. *desertipicti* as here understood. A composite of the various distinguishing specific characters must be employed to satisfactorily classify material from central Coconino County, Arizona. The former subspecies is invariably wider-leaved than the latter and its flower-color is thought to be regularly of a deeper blue-purple. All other characters are probably common to some races of each subspecies. In spite of the close approach of *P. Thompsoniae* to *P. caespitosus*, I feel that the situation is better understood by drawing a specific line at this point, for here is a boundary between major groups which are susceptible of further subdivision into geographic entities.

4. *PENSTEMON CAESPITOSUS* Nuttall ex Gray

*Penstemon caespitosus* Nutt. ex Gray, Proc. Am. Acad. 6: 66. 1862.

Stems prostrate, extensively creeping, herbaceous; leaves puberulent or occasionally glabrate, rarely exceeding 10 mm in length,  $\pm$  apiculate; inflorescence leafy, the short peduncles bearing 1-3 flowers on equally short pedicels; sepals acuminate to attenuate, puberulent, not or scarcely scarious-margined, slightly glandular; corolla nearly tubular (moderately inflated in subsp. *desertipicti*), 14-18 mm long; staminode bearded for its entire length with golden yellow hairs.

## KEY TO SUBSPECIES

Corolla nearly tubular; anther-sacs nearly as broad as long.

Leaves linear to nearly oblanceolate, puberulent with fine retrorse-spreading hairs; sepals mostly long-attenuate, 5-7 mm long.....4a. *P. c.* subsp. *typicus*

Leaves spatulate-oblanceolate to broadly obovate; sepals merely acuminate, 4-5 mm long.

Puberulence on leaves of retrorse tapering uncinat hairs; plants very low, flowers borne ca. 1 cm above ground; sepals obscurely glandular.....4b. *P. c.* subsp. *perbrevis*

Puberulence on leaves of closely appressed oblong hairs; plants somewhat higher, flowers borne 1-3 cm above ground; sepals definitely glandular...4c. *P. c.* subsp. *suffrutosus*

Corolla inflated, the throat 5-7 mm wide when pressed; anther-sacs scarcely more than half as broad as long.....4d. *P. c.* subsp. *desertipicti*

4a. *Penstemon caespitosus* subsp. *typicus* Keck, nom. nov.

*Penstemon caespitosus* Nutt. ex Gray, l.c.

Stems decumbent or assurgent, 1.5-4 or 5 cm tall, arising from slender or stout subterranean rootstocks; leaves usually puberulent, rarely nearly glabrous; corolla light blue with purplish throat, whitish within, the spreading lower lip exceeding the erect upper lip, lobes of upper lip less than 2 mm long, the throat lightly bearded within; anther-sacs broadly ovate and widely divaricate, nearly explanate; staminode densely bearded with relatively short hairs.

Occasional in southwestern Wyoming, northwestern Colorado and northeastern Utah, for the most part on sagebrush-covered slopes or flats of the Transition Zone from 1,800 to 2,600 m elevation. "Rocky Mountains, Nuttall." The type, seen at the Academy of Natural Sciences of Philadelphia, is labelled "R. Mts., N. Calif.," while a photograph shows that the isotype at Kew, a starred specimen labelled in Nuttall's hand, bears the information "R. Mts. U. Calif. Green River." The collection was doubtless made in what is now western Sweetwater County, Wyoming.

WYOMING. Yellowstone Nat'l Park: Mt. Washburn, *Biddulph* 5778 (Ph). Sublette Co. (?): between Eden and Big Piney, *Payson* 2573 (M, RM). Lincoln Co. (?): between Granger and Opal, *Payson & Armstrong* 3214 (GH, M, Ph, Po, RM). Uinta Co.: Carter, *Jones* (CI, Po); Ft. Bridger (Ph); Leroy, *Nelson* 4581 (CM, Po, RM); Evanston, *Pennell* 5895 (F, GH,

M, NY, US). Carbon Co.: Saratoga, *Buffum* 713 (F, RM); 11 mi. N. of Encampment, *Payson* 2523 (RM). COLORADO. Moffat Co.: N. of Craig, *Osterhout* 2623 (NY). Routt Co.: Egeria Park, *Eastwood* (NY, SU). Rio Blanco Co.: White River, near Wolf Creek, *Graham* 9053 (CI, CM). Jackson Co.: North Park, *Nelson* 113 (RM, SU; a glabrate form distributed under a proposed name that would emphasize its humifuse habit; but considering the glabrate material from Uinta Basin, and the variations in leaf-shape found in neighboring counties, I believe that this race has not differentiated far enough to deserve recognition). Grand Co.: Sulphur Springs, *Osterhout* 3241 (NY, SU); Willow Creek (M); Kremmling, *Porter* 2046 (CI, Ph, toward *P. Crandallii* ssp. *typicus*). Eagle Co.: McCoy's (NY); Grand River, *Osterhout* 2762 (Po, RM). Park Co.: Mount Bross, *Patterson* (CI, F, M, NY). UTAH. Uinta Co.: Dyer Mine, *Gooding* 1237 (C, F, GH, M, NY, Po, RM, SU, US); Taylor Mountain, 15 mi. N. of Vernal, *Graham* 6307 (CI, CM); Vernal-Manila road, 10 mi. N. of Vernal. *Graham* 8154 (CI, CM); Little Lake, *Graham* 8266 (CI, CM). Wasatch Co.: 3 mi. S.W. of Soldier Springs, *Graham* 9286 (CI, CM).

Keen observers will detect that material is considerably less puberulent than the average from the Uinta Basin in Utah; that the sepals are not uniformly narrowly attenuate, occasionally being more nearly acuminate in north-central Colorado; and that the leaves sometimes are spatulate-ob lanceolate in northern Colorado.

4b. *PENSTEMON CAESPITOSUS* subsp. *PERBREVIS* Pennell

*Penstemon caespitosus* subsp. *perbrevis* Pennell, Contr. U. S. Nat. Herb. 20: 375, 1920.

Stems procumbent, arising from brittle slender rootstocks, forming mats up to 5 dm across and not over 3 cm tall; leaves shorter and more abruptly expanding into the elliptic or ovate blade than in *typicus*; sepals not sharply apiculate; corolla pale lilac, the lips subequal; otherwise similar to subsp. *typicus*.

Eastern slopes of the Wasatch Mountains and sagebrush-covered plains from Duchesne County to Garfield County, Utah, at elevations of 1,600 to 2,600 m. "Collected on dry sagebrush summit of mesa, at Castle Gate, Carbon County, Utah, altitude about 2,200 to 2,400 meters, in shrivelled blossom, July 18, 1915, by F. W. Pennell (no. 6138)."

UTAH. Duchesne Co.: 14 mi. S. of Theodore (Duchesne), *Jones* (Po). Wasatch Co.: Soldier Summit, *Keck* 786 (CI, Kew, Ph, SU), *Jones* 5599 (C, M, NY, Po, RM, US). Utah Co.: P. V. Junction, *Jones* (Po); Thistle (NY, SU, US). Carbon Co.: 10 mi. E. of Colton, *Keck* 789 (CI); Castle Gate, *Pennell* 6138 (NY, type; isotypes RM, US). San Pete Co.: Wasatch

Plateau, 20 mi. W. of Castle Dale, *Keck 689* (C, CI, GH, Kew, M, Ph, Po, SU). Wayne Co.: southern part, *Dixon 300* (RM). Garfield Co.: Red Canyon (CI); Bryce Canyon (BYU).

4c. *Penstemon caespitosus* subsp. *suffruticosus* (Gray) Keck, comb. nov.

*Penstemon caespitosus* var. *suffruticosus* Gray, Syn. Fl. 2 (1): 270, 1878.

*P. suffrutescens* Rydb., Bull Torr. Club 28: 503. 1901. Based upon *P. caespitosus* var. *suffruticosus* Gray, without independent description, but applied to *Tweedy 170* from Ridgway, Colorado, which is referable to *P. Crandallii* subsp. *typicus*.

Stems decumbent, sometimes woody toward base, forming mats 1-4 dm across and up to 1 dm tall; leaves glabrous to lightly puberulent on lower surface, lightly to moderately puberulent with appressed flat hairs on upper surface, highly variable as to size; sepals and pedicels more glandular than in the other subsp., the sepals not sharply apiculate; otherwise similar to subsp. *typicus*.

Fishlake National Forest, Utah, in the Tushar Range between Beaver and Piute counties and adjacent regions, on rocky slopes in openings of the forest at elevations of 2,150 to 2,750 m. "Utah near Beaver, *Palmer*, in fruit."

UTAH. Piute Co.: mountains north of Bullion Creek, near Marysville, *Rydberg & Carlton 7106* (NY, RM, US); Gold Mt. (N. flank of Mt. Belknap), *Jones* (Po). Beaver Co.: near Beaver, 1877, *Palmer* (GH, type); 5 mi. W. of Puffer Lake, *Keck 644* (Berlin, C, CAS, CI, F, GH, Kew, M, Ph, Po, SU). Garfield Co. (?): Circle Valley Canyon, *Jones 5989n* (Po, US).

This assemblage of specimens is variable in leaf-size, amount of pubescence, woodiness of stems, and length and acumination of sepals; nevertheless it seems rightfully to compose a subspecies on the basis of its montane habitat of limited geographic extent, its restricted pubescence of singular quality, the leaf-shape and development of glands. This subspecies occurs in one of the most critical regions for the caespitose penstemons, where it is not unlikely that hybridization has been possible from time to time not only with different races from the north and south, but with those from the east and west as well, with a consequent migration of suitable genes.

4d. *Penstemon caespitosus* subsp. *desertipicti* (A. Nels.) Keck, comb. nov.

*Penstemon desertipicti* A. Nels., Univ. Wyo. Pub. Bot. 1: 130. 1926.

Stems procumbent, the spreading rootstocks scarcely woody, often forming broad mats, rarely over 3 cm tall; leaves linear-oblancoelate to lance-obovate, densely puberulent with spreading retrorse hairs; leaves and sepals  $\pm$  sharply

apiculate; corolla usually abruptly (sometimes slightly) inflated, the limb blue but like the throat pale externally, the throat whitish, sometimes with fine guide lines, very shallowly plicate, the orifice usually more densely pubescent and the staminode with a denser longer beard than in the preceding subsp.; anther-sacs ovate-oblong, relatively deep.

Garfield County, Utah, to Coconino County, Arizona. "The type number is A 177, secured by *Herbert C. Hanson*, near Cameron, Arizona, Aug. 25, 1922, on a limestone plateau, altitude about 5000 ft."

UTAH. Garfield Co.: Bryce Canyon, *Goodman & Hitchcock 1561* (C, F, M, NY, SU); entrance to Bryce Park (Utah); Ruby Lodge (CAS); Tropic, *Jones 5312ai* (US). Kane Co.: Greenhilde Ranch, 25 mi. S. of Panguitch, *Eggleston 10188* (US). ARIZONA. Canyon of the Colorado, *Purpus 8176* (C). Coconino Co.: S. of Montezuma Point, Grand Canyon, *Degener 4478* (NY); Anita Camp, June 1901, *Bicknell* (US); Cameron, *Hanson A 177* (RM, type; isotypes F, M, NY); Painted Desert, N.E. of Flagstaff, *Hanson B-177* (RM); S. Rim, 50 mi. S. of Grand Canyon, *Maguire & Piranian 12222* (CI, Ph, Utah); Flagstaff, *MacDougal 211* (C, F, GH, NY, US). Navajo Co.: Cedar Springs, *Toumey 370* (UARiz, US).

In spite of the considerable list of characters given in the description above, this group of plants cannot retain specific rank on the basis of our present knowledge. The material examined varies in corolla-size and -shape, leaf-size and -shape, to some extent in habit, anthers, bearding of the throat and staminode, and so on. Plants within single collections show some of this variability, including those of the type collection. Apparently this subspecies is distributed in a manner similar to the remainder of the species, quite discontinuously, thus permitting local races to become established that differ in minor characters. This subspecies approaches very closely to subsp. *perbrevis* and *suffruticosus* in morphological characters in the northern part of its range and the Bryce Canyon material is largely intermediate in character between this and the former subspecies. The specimen cited by Nelson as a paratype (*Jones 4658*) is here classed as *P. Thompsoniae* subsp. *typicus*.

##### 5. *PENSTEMON ACAULIS* Williams

*Penstemon acaulis* Williams, Ann. Miss. Bot. Gard. 21: 345. 1934.

Rootstocks subterranean, largely herbaceous, branching very short, terminated by dense tufts of narrowly linear greenish leaves; leaves broadest above the middle, acutish, not mucronate, glabrate or scabrous with spiculate hairs,  $\pm$  viscid, 15–22 mm long; flowers solitary, sessile; the long acuminate glutinous sepals hidden in the foliage; corolla deep azure blue, 14–16 mm long, moderately amplate, the prominent limb up to 10 mm wide, strongly golden bearded within the throat; staminode bearded throughout.

"Collected in flower on dry hilltops near McKinnon, Sweetwater Co., Wyoming, altitude about 6,500 feet, May 28, 1932, *Williams 407*." Known from only the vicinity of the type collection in Sweetwater County, Wyoming, and in adjacent portions of Daggett County, Utah (personal communication from Williams).

WYOMING. Sweetwater Co.: McKinnon, *Williams 407* (RM, type; isotypes CAS, M, NY, Ph). (UTAH. Daggett Co.: Antelope, Aug. 2, 1936, *Alexander, Everett & Cutting*; and southeast of Manila—fide L. S. Williams.)

This local endemic is amply distinct from *P. caespitosus* subsp. *typicus*, with which it is most closely associated both geographically and morphologically. The character of its pubescence is unique in this group of species. In addition, it is marked by relatively large, solitary corollas of deep color, no aerial stem, and the absence of mucros on leaves and sepals.

As this goes to press, Dr. F. W. Pennell sends me an illuminating ecological note by Mr. E. J. Alexander, of the New York Botanical Garden who collected this species at Antelope. He observed that the plants are not truly acaulescent, for his specimens showed stems of several years preceding growth, bearing old leaves and capsules, buried underground. Alexander states that the stems are annually buried under soil wash. His fruiting specimens show that the capsules, which are 3 mm long and shorter than the calyx, are indehiscent and long persistent, as was found when plants were dug up. Those with the seed still intact were found in the branch axils of two to five years previous. He reports that the unusually shaped lunate-reniform seeds are set free by decay underground and increase the plant by germination in situ, a unique occurrence in *Penstemon*.

#### 6. *PENSTEMON CRANDALLII* A. Nelson

*Penstemon Crandallii* A. Nels., Bull. Torr. Club 26: 354. 1899.

Stems ascending or erect, from suffrutescent spreading rootstocks; leaves linear to oblanceolate or spatulate, glabrate (except in subsp. *atratus*), the principal ones 12–30 mm long; inflorescence  $\pm$  leafy, usually secund, glandular-puberulent; corolla dark blue-purple, nearly tubular, 14–22 mm long, moderately bearded on the ridges of throat at orifice, deeply 2-lipped, the lower lip exceeding the upper; anther-sacs ovate; staminode golden bearded.

#### KEY TO SUBSPECIES

Stems ascending-erect; leaves linear to oblanceolate, acute to bluntly obtuse, gradually tapering to the base, glabrous apically.

Leaves linear-oblanceolate, moderately crowded.....6a. *P. C.* subsp. *typicus*

Leaves narrowly linear or nearly so, more densely crowded.....6b. *P. C.* subsp. *glabrescens*

Stems decumbent; leaves spatulate (the upper oblanceolate in subsp. *atratus*), more abruptly petiolate.

- Leaf-blades glabrous, elliptic to obovate, drying green . . . . . 6c. *P. C.* subsp. *procumbens*  
 Leaf-blades scabrid-puberulent, oblanceolate-oblong, drying blackish . . . . .  
 . . . . . 6d. *P. C.* subsp. *atratus*

6a. ***Penstemon Crandallii* subsp. *typicus* Keck, nom. nov.**

*Penstemon Crandallii* A. Nels., l.c.

*P. xylus* A. Nels., Bot. Gaz. 34: 31, 1902. Proposed as a new name for *P. caespitosus* var. *suffruticosus* Gray (= *P. caespitosus* subsp. *suffruticosus* (Gray) Keck), but fully described and a specimen cited, which must stand as the type. "The specimens before me were collected by Mr. H. N. Wheeler at Sapinero, Colo., 1898, no. 446." The type collection is composed of specimens with unusually slender stems and long internodes.

Stems ascending-erect, tufted; leaves linear-oblanceolate, usually glabrous above the petiole; sepals narrowly scarious-margined, acuminate to attenuate, 4-6 mm long; corolla 17-22 mm long, the lower lip 5-7 mm long.

Frequent from Teller County, Colorado, to San Juan County, Utah, usually on dry, brush-covered slopes, at elevations of 1,800 to 3,050 m. "I am indebted to Prof. C. S. Crandall for specimens of this plant, collected by him near Como, Park County, Colorado, July 23, 1897."

COLORADO. Teller Co.: Cripple Creek, *Schedin* 714 (RM). Gilpin Co.: Central City, *Schedin* 764 (RM). Park Co.: Como, July 23, 1897, *Crandall* (RM, type; isotype C), 4197 (NY, 4198 (F, Ph, RM, US); Estabrook (CM). Chaffee Co.: South Cottonwood Gulch, *Sheldon* 547 (Minn, NY, US). Gunnison Co.: Sapinero, *Wheeler* 446 (RM, type of *P. xylus*; isotype NY). Hinsdale Co.: Lake City, *Purpus* 721, in part (F). Archuleta Co.: Chromo, *Porter* 2024 (CI). Ouray Co.: Ouray (NY); Ridgeway, *Payson* 3830 (C, GH, M, Ph, RM, SU), *Tweedy* 170 (NY, the only specimen cited by Rydberg under his *P. suffrutescens*, US). Montrose Co.: Cimarron, *Baker* 333 (C, F, GH, M, Minn, ND, NY, Po, RM, SU, US); Cerro (ND); Tabeguache Basin, *Payson* 3873 (C, GH, M, Ph, RM, SU). Delta Co.: Paonia, *Osterhout* 4523 (NY); Milk Creek near Mesa Grande, *Purpus* 214 (F). Mesa Co.: 2 mi. S. of Mesa, *Keck* 805 (CAS, CI, Ph, SU); 5.5 mi. S. of Mesa, *Keck* 812 (CI, Ph, SU). UTAH. San Juan Co.: Elk Ridge, Abajo Mts., *Maguire & Redd* 2078 (CI, Utah), 2079 (Utah).

A specimen from Sapinero, *Pennell* 6269 (NY), I believe is a hybrid between this subspecies and *P. leucrioides*, with which it was growing.

In proposing *P. xylus*, Nelson made no comparisons with his previously published *P. Crandallii*. But with insufficient material from the region it would have been difficult at that time to ascertain the true identities of the two. *Pennell*<sup>1</sup> attempted to separate the two proposals on a basis of

<sup>1</sup> Contr. U. S. Nat. Herb. 20: 334-335, 1920.

flower-size, but this and other characters tried fail to be of any significance when more abundant collections are studied. In fact, there is scarcely a trend of flower-size difference in this subspecies from one extreme of its range to the other.

6b. *Penstemon Crandallii* subsp. *glabrescens* (Pennell) Keck, comb. nov.

*P. glabrescens* Pennell, Contr. U. S. Nat. Herb. 20: 375. 1920.

Stems ascending-erect, tufted; leaves linear, usually glabrous above the petiole, more crowded than in *typicus*; sepals usually more prominently scarious-margined, attenuate; corolla 15–20 mm long, otherwise like *typicus*.

Southwestern Colorado and adjacent New Mexico, on dry hillsides from 2,100 to 2,750 m elevation. "Collected on open mesas and gravelly hillsides at Pagosa Springs, Colorado, in flower, July 2, 1917, by E. Bethel."

COLORADO. Fremont Co.: Canon City, 1874, *Brandege* (Ph); Lock Mt., *Rollins* 1229 (CI); Sangre de Cristo Pass, *Brandege* 806 (C, M, Ph). Custer Co.: Wet Mountain Valley (Ph); Rosita, *Brandege* (C.) Saguache Co.: Brewery Creek Ranger Station, *Rollins* 1315 (CI). Mineral Co.: Caldwell Creek, *Murdock* 4578 (F, M, NY, US); Goose Creek (F, Po); Wagonwheel Gap, *Smith* (Ph); Wolf Creek Pass, *Bethel*, *Willey & Clokey* 4280 (NY, Ph, RM). Archuleta Co.: Pagosa Springs, July 2, 1917, *Bethel* (NY, type), *Bethel et al.* 4266 (C, CAS, F, M, Minn, NY, Ph, Po, RM, SU, US); Piedra (Ph). La Plata Co.: Bayfield, *Bethel* (NY); Durango, *Eastwood* 5363 (CAS). Montezuma Co.: E. of Mancos, *McKelvey* 4659 (CI, Ph); Mancos, *Baker, Earle & Tracy* 27 (F, GH, M, ND, NY, Minn, Po, RM, US); Lone Mesa, *Cary* 197 (US). NEW MEXICO. Taos Co.: N. of Taos, *Castetter* 1716 (RM). Rio Arriba Co.: Dulce, *Standley* 8229 (US); Ensenada (US); S. of Tierra Amarilla (NY, US).

This subspecies is not sharply differentiated from subsp. *typicus* on the one hand, nor from *P. linarioides* subsp. *coloradoensis* on the other. Each of the distinctive characters of *glabrescens* is occasionally carried over into one of the other two by hybridization.

6c. *Penstemon Crandallii* subsp. *procumbens* (Greene) Keck, comb. nov.

*P. procumbens* Greene, Pl. Baker. 3: 23. 1901.

Stems decumbent,  $\pm$  suffrutescent, often forming broad mats and up to ca. 1 dm tall; leaves glabrous on both surfaces, their petiolate bases usually finely and retrorsely puberulent, their blades abruptly elliptic to obovate; sepals obscurely scarious-margined, acute to acuminate, sparingly glandular; corolla 14–17 mm long, the lower lip 3–4 mm long.



Northwestern Gunnison County, Colorado, at *ca.* 3,050 m elevation. "Forming large mats on open slopes at Keblar Pass, 7 Aug. [1901, C. F. Baker] n. 733."

COLORADO. Gunnison Co.: Ragged Mountain, *Cowen* (GH); Mount Carbon, *Clawson* 5741 (US), *Brandege* (C); Elk Mts., *Brandege* (M); Keblar Pass, *Baker* 733 (ND, type; isotypes C, GH, M, NY, Ph, Po, RM, SU, US), June 24, 1910, *Clawson* (NY).

In recent years this material has been called *P. suffrutescens* Rydb. This name must go into synonymy under *P. caespitosus* subsp. *suffruticosus* (Gray) Keck as shown, but the specimen cited by Rydberg, which was a basis of his conception of *P. suffrutescens*, is now cited as *P. Crandallii* subsp. *typicus*. This specimen, *Tweedy* 170, is incomplete, but appears to differ from subsp. *procumbens* in habit and leaf-shape. It is a good match for material of *typicus* from Delta and Mesa counties.

The characters listed for this subspecies might appear to warrant its retention on a specific basis. Adequate flowering specimens, however, have yet to be studied before one can emphasize corolla characters, and there is an obvious similarity between the present collections and those of *typicus* taken in the region to the west. Further field study is highly desirable for a better understanding of *procumbens*, but at present it appears that this group has not attained sufficient isolation from *typicus* to warrant specific rank for it.

The most variable features appear to be sepal-length and leaf-size, the width of leaf-blades at the widest point varying from 3 to 7 mm.

A strong resemblance is evident between this subspecies and extreme forms of *P. caespitosus* subsp. *suffruticosus* that may be superficial or of a genetic nature. The principal difference between them concerns the puberulent upper surface of the leaf in the latter in contrast with the glabrous blade of the former. Each of these subspecies is connected with typical material of its respective species by a complete series of intergrades. This fact, together with a consideration of the broad geographic separation existing between the subspecies, suggests that theirs has been a parallel variation. It is likewise possible, however, that these are of recent monophyletic origin, and that by some chance agency the race was transferred from its seat of origin to the new locality where opportunity was afforded it to be influenced to some extent by its association with the native strains.

6d. *Penstemon Crandallii* subsp. *atratus* Keck, subsp. nov.

Rhizoma parce suffrutescens et repens; ramis confertis e basi adscendentibus vel decumbentibus 3–10 cm longis; foliis usque ad 18 mm longis 5 mm latis oblanceolato-spatulatis utrimque scabro-puberulis atratis, apicibus argutis

obtusis vel rotundatis; sepalis oblongo-lanceolatis sensim acuminatis viscido-puberulissimis margine obscure scarioso; corolla 16–19 mm longa 5 mm lata, limbo patenter bilabiato, inferiore 4 mm longo.

Type: *Marcus E. Jones* (Dudley Herb. of Stanford University, no. 158171), collected in the La Sal Mountains, Utah, June 2, 1914; isotypes C, CAS, CI, F, GH, NY, Po, SU, US.

Known in typical form only from the La Sal Mountains which lie across the line between Grand and San Juan counties in southeastern Utah. Two other collections are at hand referable to this subspecies; one is *Purpus* 6593 (C, M, Po, US), taken in oak brush in the La Sal Mountains, June 1899, between 2,150 and 2,450 m altitude. In about half of the specimens in this collection the leaf-blades are glabrous, although in other characters they closely match the type collection. The other collection is from Naturita, Montrose Co., Colo., *Payson* 361 (RM). This is definitely scabrid-puberulent throughout, but in the color of its foliage and habit it approaches subsp. *typicus*.

The proposed subspecies appears to represent a valid ecotype of *P. Crandallii*, as shown by neighboring collections of this species, rather than of *P. caespitosus* to which it has been referred in herbaria. The scabrous puberulence of the leaves recurs in *Crandallii typicus* from adjacent Montrose County, as shown in some plants of *Payson* 3873 from Tabeguache Basin.

There is also an evident similarity between subsp. *atratus* and *P. retrorsus* of Montrose County, that leads to speculation about whether the former might not have arisen through hybridization between *P. retrorsus* and *P. Crandallii typicus*.

#### 7. PENSTEMON ABIETINUS Pennell

*Penstemon abietinus* Pennell, Contr. U. S. Nat. Herb. 20: 376. 1920.

Stems ascending-erect, 5–12 cm tall, tufted, from horizontal suffrutescent rootstocks forming small clumps or mats to 1 m in diameter; leaves linear, mucronate, crowded, glabrous at least apically, mostly 1 cm long and 1 mm wide, plane or folded along the midrib; calyx-lobes lance-acuminate with expanded undulate-erose scarious margin at base, not puberulent but sparingly pubescent with gland-tipped hairs; corolla 14–18 mm long, up to 5 mm wide when pressed, deep blue or ultramarine with red-purple tube, without guide lines in the orifice and very sparingly bearded on the palate, deeply 2-lipped, the lips sub-equal; anther-sacs ovate, 1 mm long; staminode regularly bearded with orange-yellow hairs throughout.

On open slopes and banks in deep soil, occurring as scattered colonies, Sevier County, Utah, at elevations of 2,100 to 2,600 m. "Collected at Ire-

land Ranch, head of Salina Canyon, Utah, altitude 2,400 meters, in flower, June 15, 1894, by Marcus E. Jones (no. 5440)."

UTAH. Sevier Co.: Ireland Ranch, head of Salina Canyon, *Jones 5440* (US, type; isotypes C, F, GH, M, NY, RM); Sawtooth, 15 mi. up Salina Canyon, *Keck 681* (C, CAS, CI, GH, Kew, Ph, Po, SU); Salina Experiment Station, *Keck 672* (Berlin, C, CAS, CI, M, Ph, Po, SU), *Eggleston 11138* (US).

Pennell proposed this species contemporaneously with *P. glabrescens* (= *P. Crandallii* subsp. *glabrescens*). In his key, the sole character presented to differentiate the two is corolla-size. However, more abundant material of *P. abietinus* now discloses that it has corollas just as large as the average collection of *P. Crandallii* subsp. *glabrescens* and that the character lacks even secondary importance. There is, of course, a rather substantial geographic gap between *P. abietinus* and the latter that magnifies the importance of any differences between the two which may be found as inter-crossing is prevented. The only differences I can find to support the geographic isolation and retain *P. abietinus* as distinct from *glabrescens* are the absence of guide lines in the corolla and the near-absence of beard in the throat. The lengthy specific diagnoses provided by Pennell did not mention these, and have uncovered no additional unique characters. He had very poor flowering material of *P. abietinus* before him at the time he was describing it.

One finds it almost equally difficult to separate the present species from *P. linarioides* subsp. *Sileri* and the var. *viridis* which occur in Southern Utah. The important characters here are found in the beard of the staminode, which is bright yellow and sparse in *Sileri* except for the long and dense apical tuft, whereas in *abietinus* the beard is uniformly orange-yellow, dense and short throughout.

*Penstemon abietinus* must be considered a very poorly defined species at present, but it appears to have attained complete isolation and the complex situation existing in this portion of the genus is doubtless clarified by recognizing this unit as a species. Confusion would result from an attempt to attach it to either of the above named species with which it is closely related; and certainly we would not clarify matters by combining the three under one taxonomic species, for we would then have a swarm of recognizable subunits, some of which would be entirely dissimilar.

#### Subsection 2. *Linarioides*, new subsection

Stems ascending or erect from a non-creeping rather stout woody caudex, 1-5 dm tall, pubescent; leaves linear or broader; corolla externally viscid, tubular-campanulate, prominent guide lines usually present about orifice, the upper and lower lips about equal and spreading.

## KEY TO THE SPECIES OF LINARIOIDES

Corolla 14–24 mm long, blue-purple; leaves 8–20 (–30) mm long, not fleshy, grayish or greenish on both surfaces.

Leaves linear (ob lanceolate in subsp. *Maguirei*); corolla tubular-campanulate, 16–24 mm long, prominently bearded at orifice and with strong guide lines. . . . . 8. *P. linarioides*

Leaves linear-ob lanceolate; corolla narrowly tubular-funnelform, 14–18 mm long, weakly bearded at orifice and without strong guide lines. . . . . 9. *P. californicus*

Corolla 10 mm long, white tinged with lavender; leaves 5–8 (–10) mm long, fleshy, white-puberulent on the flat upper surface, deep green on the rounded lower surface. . . . . 10. *P. discolor*

8. *PENSTEMON LINARIOIDES* A. Gray

*Penstemon linarioides* A. Gray, in Torr., Bot. Mex. Bound. 112. 1859.

Stems from a multicapital suffruticose caudex (from a short rootstock in subsp. *compactifolius*), leafy throughout; herbage cinereous-pubescent throughout or the leaves glabrous; leaves linear (ob lanceolate in subsp. *Maguirei*), mucronate; calyx-lobes broadly ovate with acute to acuminate tip, sometimes ovate-oblong, the margin prominently scarious and entire or erose; corolla tubular-campanulate, definitely ampliate, bright blue with purplish tube to lavender, prominent guide lines in the 2-ridged throat, the palate  $\pm$  strongly bearded, 16–24 mm long, 5–8 mm wide (pressed); anther-sacs ovate-oblong, deep; staminode bearded almost throughout its length (except in subsp. *coloradoensis*) with bright yellow or golden yellow hairs.

## KEY TO SUBSPECIES AND VARIETIES

## A. Leaves essentially linear.

## B. Puberulence of leaf-blades of fine erect or retrorsely spreading crowded hairs, or none.

Floral leaves not diminished in size; calyx-lobes 6–8 mm long, ovate with long acuminate tips. . . . . 8a. *P. l.* subsp. *taosensis*

Floral leaves abruptly diminished in size; calyx-lobes 5–6 mm long.

Leaves densely puberulent. . . . . 8b. *P. l.* subsp. *Sileri*

Leaves essentially glabrous. . . . . 8c. *P. l.* var. *viridis*

## BB. Puberulence of leaf-blades of flattened scale-like closely appressed hairs.

Staminode sparsely bearded with short hairs, principally confined to an apical tuft; plants 1.5–3 dm tall. . . . . 8d. *P. l.* subsp. *coloradoensis*

Staminode more densely bearded with longer hairs for most of its length.

Stems ascending from a decumbent or short rootstock; leaves closely overlapping, heathlike, mostly 1 cm long. . . . . 8e. *P. l.* subsp. *compactifolius*

Stems strictly erect from the compact caudex; leaves rarely closely crowded, longer. . . . . 8f. *P. l.* subsp. *typicus*

AA. Leaves principally oblanceolate. . . . . 8g. *P. l.* subsp. *Maguirei*

8a. *Penstemon linarioides* subsp. *taosensis* Keck, subsp. nov.

Folia cinereo-puberula vel glabrata; foliis inflorescentiis vix reductis modice recurvis; sepalis late ovatis margine membranaceis acumine subulato terminatis, 6–8 mm longis.

Type: *Aven Nelson & Ruth A. Nelson no. 158* (University of California, no. 500219), collected between Questa and Taos, Taos County, New Mexico, July 30, 1932; isotypes M, RM.

Additional collection: Taos Canyon, 7 mi. E. of Taos, *Wilkins* 2434 (Ph).

This subspecies is confined to Taos Co., New Mexico, so far as known, but certain collections from Rio Arriba Co., such as *Eggleston* 6549, in part, from hills south of Tierra Amarilla, appear to be closely related.

The type collection is marked by a sparse, very fine puberulence of falcate hairs on the leaves, while the Wilkins collection has glabrous leaves. Thus in pubescence alone subsp. *taosensis* may be distinguished from the only other form of the species in the region, subsp. *coloradoensis*. The latter also has less beard on the staminode. From *P. Crandallii* subsp. *glabrescens*, the present subspecies is distinguished by its more ampliate corolla and by its taproot.

8b. *Penstemon linarioides* subsp. *Sileri* (A. Gray) Keck, comb. nov.

*Penstemon linarioides* var. *Sileri* A. Gray, Syn. Fl. 2(1): 270. 1878.

*P. coloradoensis* subsp. *Sileri* Pennell, Contr. U. S. Nat. Herb. 20: 363. 1920.

Leaves densely puberulent with fine erect or moderately retrorse hairs; staminode often sparsely bearded below the apical tuft.

Common from Iron County, Utah, and adjacent Nevada, to Yavapai County, Arizona; rare farther south to Cochise County, Arizona. "S. Utah, *Siler, Parry*."

UTAH. S. Utah, *Parry* 151 (GH, cotype), 1874, *A. L. Siler* (GH, type), probably isotype from Osmer, *Siler* 90 (M). Iron Co.: Cedar Canyon, *Garrett* 2952 (Ph), Cedar Canyon, South Fork (Ph); E. of Cedar Breaks (Ph). Kane Co.: Irish Valley, *Jones* (Po); Long Valley, *Cottam* 4276 (Ph); Orderville, *Jones* 25541 (M, Po, SU); 5 mi. W. of Mt. Carmel junction (CI, Ph, Utah); Mt. Carmel to Zion, *Eastwood & Howell* 1131 (C, CAS, CI); Sink Valley (C, US); Kanab (CAS). Washington Co.: Pine Valley, *Eastwood & Howell* 1267A (CAS, CI, SU); Pine Valley Mts., *Maguire & Richards* 13112 (CI, Ph, Utah); St. George, *E. Palmer* (NY). NEVADA. Lincoln Co.: between Pioche and Geyser, *Jaeger* (CI). ARIZONA. Coconino Co.: Kaibab Plateau near Jacobs Lake, *Eastwood & Howell* 1123, in part (CAS, CI, SU); 12 mi. N.W. of Jacobs Lake (CAS); El Tovar, Grand Canyon, *Eastwood* 5675 (CAS); 11.9 mi. W. of Williams, *Goddard* 520 (C); Flagstaff, *Jaeger* (Po). Mohave Co.: Cane Spring Mts. (labelled Utah), *Purpus* 6227 (C, US); Hualapai Mts., *Jones* (Po). Yavapai Co.: Beaver Creek, 20 mi. above Camp Verde, *Wolf* 2430, in part (CAS, SU); Ft. Verde, *Rusby*, in part (C, CI, F, M, NY, US); 4 mi. W. of Prescott, *Wolf* 2318 (CAS, GH, SU); Prescott, *Fulton* 7220 (NY, Po); Bradshaw Mts. (SU); S. of Ash Fork, *Toumey* 367 (SU, US, UAriz). Gila Co.: Sierra

Ancha, *Harrison & Kearney 5658*, in part (Ph, US); Black River, *Goodding 1102*, in part (NY, RM, US); Globe (SU). Cochise Co.: Dragoon Summit, *Thorner 2605* (CI); Outlaw Canyon, Chiricahua Mts., *Goodding 2351* (C, M, NY, RM).

8c. *Penstemon linarioides* var. *viridis* Keck, var. nov.

Subsp. *Sileri* similis; foliis glabris.

Type: *Roxana S. Ferris & Carl D. Duncan no. 2278* (Dudley Herb. of Stanford University, no. 124333), collected near Bright Angel Camp, Grand Canyon, Coconino County, Arizona, June 16, 1921.

Frequent over the range of subsp. *Sileri*.

UTAH. Kane Co.: Irish Valley, *Jones* (CI, Po); 5 mi. W. of Mt. Carmel junction, *Maguire & Piranian 12304* (Utah). Washington Co.: Zion Canyon, *Jones* (Po.) ARIZONA. Coconino Co.: Kaibab Forest, *Goodman & Hitchcock 1657*, in large part (C, CAS, F, M, NY, Ph, SU); Grand Canyon, Bright Angel, *Jones* (Po); El Tovar, Grand Canyon, *Eastwood 3773* (CAS); 2 mi. S. of Yaki Point, *Borell* (C); Flagstaff, *Rusby 769*, in part (C); Oak Creek Canyon (CI). Mohave Co.: Mt. Delenbaugh, *Cottam et al. 4144* (Ph). Yavapai Co.: Beaver Creek, 20 mi. above Camp Verde, *Wolf 2430*, in part (GH, Po). Gila Co.: Mercury Mine, *Eastwood* (CAS).

This unit is kept in varietal rank because of its spasmodic occurrence, although in the vicinity of Grand Canyon it appears to be the dominant form. Also, var. *viridis* as here circumscribed undoubtedly is a derivative of subsp. *Sileri*, with which it entirely agrees in distribution and from which it differs only in having glabrous leaves. In spite of this evident relationship I prefer to maintain the variety as a trinomial. In addition to avoiding the quadrinomial, this has the additional advantage of accommodating some material with glabrescent leaves from farther south in Arizona should it ultimately be placed here, although at present it seems to be of different derivation.

8d. *Penstemon linarioides* subsp. *coloradoensis* (A. Nels.) Keck, comb. nov.

*Penstemon coloradoensis* A. Nels., Bull. Torr. Club 26: 355. 1899.

Stems many, rarely exceeding 3 dm in height; leaves  $\pm$  crowded, always puberulent with closely appressed hairs; flowers moderately crowded, corolla lightly bearded at orifice; staminode prominently bearded apically with bright yellow hairs, and sparsely bearded dorsally with shorter whitish or yellowish hairs or nearly glabrous.

Common on plains and foothills with sagebrush, pinyon, juniper and oak, in southwestern Colorado and northwestern New Mexico. "Mancos, Colorado, by Messrs. Baker, Earle and Tracy, 1898."

COLORADO. La Plata Co.: Hermosa, *Bethel* (NY); 10 mi. E. of Durango, *Porter 2030* (CI); Durango, *Crandall 1826* (F, NY, Ph, RM, US). Montezuma Co.: Dolores, *Crandall* (NY); Mancos, *Baker, Earle & Tracy 70* (RM, type of *P. coloradoensis*; isotypes C, CAS, F, GH, M, NY, Ph, Po, US); Mesa Verde, S. of Cortez, *Payson 1129* (NY, RM); Mesa Verde Nat'l Park, *Goodman & Hitchcock 1361* (C, F, NY, SU). NEW MEXICO. Rio Arriba Co.: Rosa, *Baker 600* (GH, M, NY, Po, RM, US). San Juan Co.: Carrizo Mts., *Matthews* (GH, US); Tunicha Mts., above Toadlena, *McKelvey 4617* (CI, Ph).

No basis has been found for retaining *coloradoensis* as a species. In fact, the principal distinction between it and subsp. *typicus* is the amount of beard on the staminode. The importance placed in such a quantitative character is justified only as it is constant and as it is correlated with less tangible differences in height, flower-size, length of internodes, and so on. In spite of the rather trifling differences between these two subspecies, they do not seem to overlap in distribution or have resultant puzzling intergrades.

8e. *Penstemon linarioides* subsp. *compactifolius* Keck, subsp. nov.

Caudex plus minusve repens; caulibus erectis; foliis imbricatis confertis adpresso-puberulis plerumque 1 cm longis.

Type: *D. T. MacDougal no. 32* (New York Botanical Garden), collected in the vicinity of Flagstaff, Coconino Co., Arizona, June 3, 1898, at 2,130 m altitude; isotypes C, CI, F, GH, M, Ph, RM, US.

This subspecies is limited to the vicinity of Flagstaff, where it is the most abundant sort of the species. Fifteen independent collections of it from Flagstaff have been available for study, one from Walnut Canyon ranger's cabin and one from Oak Creek. This subspecies and var. *viridis* from the vicinity have an appearance in common, both being heathlike, or their closely packed rigid leaves give the branches an aspect like spruce or fir twigs. Subsp. *compactifolius* marks the northernmost outpost in central Arizona for the occurrence of the closely appressed puberulence on the leaves that marks the material to the south and east. In the Flagstaff region intergrades occur between this and subsp. *Sileri* and the var. *viridis*.

8f. *Penstemon linarioides* subsp. *typicus* Keck, nom. nov.

*Penstemon linarioides* A. Gray, l.c.

Stems several, to 5 dm tall; leaves not densely crowded except at base of stems or on short sterile shoots,  $\pm$  as long as the internodes on flowering stems, dealbate-puberulent, the hairs on blades closely appressed; corolla

16–20 mm long, rather strongly bearded at orifice; staminode well bearded for almost its entire length but the hairs at apex often longer.

Frequent in canyons and foothills of the Upper Sonoran and lower Transition zones, at 1,370 to 1,830 m elevation, in western New Mexico and southeastern Arizona. "Organ mountains; *Parry*. Copper Mines and Los Animas, New Mexico; *Wright*, (1472), *Thurber*, (331, 1115), *Bigelow*. Sierra San Luis, Chihuahua and Sonora; *Schott*." Apparently the only *Parry* specimen from the Organ Mountains before Gray at the time he proposed this species was from the Torrey Herbarium, as none is preserved in the Gray Herbarium. This fragment consists of but one inflorescence with a single flower. Since Gray was not working with the present day type concept in mind, we may be permitted to select the second specimen cited, *Wright* 1472, at the Gray Herbarium, to stand for the type of the species in place of the wholly inadequate *Parry* specimen. Both represent the same form of the species, and *Wright* 1472 is not only a good collection but is distributed in duplicate to several herbaria. In addition, *Thurber* 1115, also cited by Gray, is from the same locality, Cobre (or Copper Mines), which at the present day is known as Santa Rita and is in eastern Grant Co., New Mexico.

NEW MEXICO. McKinley Co.: Fort Wingate, *Matthews* (GH); Coolidge, *Tracy* (F); Gallup to Zuni, *Hawver* (CAS); Fort Defiance (NY). Socorro Co.: Socorro, *Plank* (NY); Wheeler's Ranch, *Wooton* (C, NY, Po, SU, US); Water Canyon, Magdalena Mts. (F). Catron Co.: Tularosa Creek, *Goddard* 828 (C, F); Luna, *Wooton* (M, US); Mogollon Mts., *Rusby* 326 (F, M, NY). Grant Co.: Mangas Springs, *Metcalf* 160 (M, NY, RM, US); 4 mi. E. of Gila, *Maguire et al.* 11618 (Utah); 516 Ranch, Mogollon Creek, *Maguire et al.* 11964 (Ph, Utah); Silver City, *Mulford* 835 (M, NY, Ph); Cobre (now Santa Rita), *Wright* 1472 (GH, type; isotypes M, NY, Ph), *Thurber* 1115, in part labelled Copper Mines (GH, NY); San Luis Mts., *Mearns* 2203, 525 (US). Dona Ana Co.: Organ Mts., April 29, *Parry* (NY), *Standley* (M, US); Fillmore Canyon, Organ Mts., *Wooton* (NY, RM, US). Hidalgo Co.: Los Animas, *Thurber* 331 (GH, NY, US). ARIZONA. Apache Co.: Concho, *Wooton* (US). Navajo Co.: Heber (CI); Pinedale, *Hough* 111 (US); Fort Apache (GH). Gila Co.: Tonto Natural Bridge (CI); Mercury Mine, Mazatzal Range, *Eastwood* 17255 (CAS); Summit Ranch, Natanes Plateau, *Goodding* 699 (GH, NY, RM, US); Apache Mts., 25 mi. from Rice, *Ferris* 1292 (SU); Cassadero Springs, *Maguire et al.* 13040 (Ph, Utah); Black River, *Goodman & Hitchcock* 1289 (C, CAS, F, M, MY, Ph, SU). Graham Co.: 10 mi. W. of Ash Creek Ranch, *Maguire et al.* 13073 (Ph, Utah). Greenlee Co.: 2 mi. N. of Metcalf, *Maguire et al.* 13073 (Ph, Utah). Cochise Co.: Apache Pass, *Lemmon* 417, 255



(C, GH); Bowie, *Jones 4293* (F, NY, Po, SU, US, Utah); Pinery Canyon, Chiricahua Mts., *Stone 632, 820* (Ph); Portal, *Eggleston 10948* (GH, US); Fort Huachuca, *Lemmon 2853* (C, GH).

8g. *Penstemon linarioides* subsp. *Maguirei* Keck, subsp. nov.

Subsp. *typicus* similis; foliis oblanceolatis inferis 2.5–5 mm latis obtusis ad basim longe acuminatis.

Type: *Maguire, Richards & Moeller no. 11797* (Utah State Agricultural College Herbarium, no. 18872), collected on limestone cliff sides 1 mi. W. of Metcalf, Greenlee County, Arizona, June 5, 1935; isotypes CI, Ph.

Known only from the Gila Valley of southeastern Arizona and adjacent New Mexico.

NEW MEXICO. Grant Co.: Gila Valley, Nov. 1880, *Greene* (Po). ARIZONA. Greenlee Co.: Metcalf, *Davidson 87* (GH).

9. *Penstemon californicus* (M. et J.) Keck, comb. nov.

*Penstemon linarioides* var. *californicus* Munz et Johnst., Bull. So. Calif. Acad. Sci. 23: 31. 1924.

Stems 5–15 dm tall, from a multicipital woody caudex or decumbent short rootstock, densely leafy below, the inflorescence less leafy; herbage cinereous-puberulent throughout with closely appressed flattened white hairs, pallid; leaves linear-ob lanceolate, the largest 8–15 mm long, 1.5–2.5 mm wide, mucronate, thickish, the upper surface usually whiter; calyx-lobes ovate, acute to acuminate, the margin entire, scarious; corolla narrowly tubular-funnelform, moderately ampliate, purplish blue, 14–18 mm long, 4.5–6 mm wide (pressed); anther-sacs ovate-oblong, deep; staminode yellow-bearded almost throughout its length or chiefly apically.

Upper Sonoran Zone from San Jacinto Mts., California, to San Pedro Martir Mts., Baja California. "Munz & Johnston 5445, Kenworthy, Hemet Valley, San Jacinto Mts."

CALIFORNIA. Riverside Co.: 2 mi. below Kenworthy, Hemet Valley, *Munz & Johnston 5445* (Po, type; isotypes C, GH, RM, SU), *Munz 5976* (Po); Aguanga (labelled San Diego County), *Parish 1388* (C, GH, Ph, SU, US). MEXICO. Baja California: Cantillas Mts., *Orcutt 893* (C, GH, US), July 14, 1884, *Orcutt* (C), July 5, 1884, *Orcutt* (CM, US); 50 mi. S.E. of Tecate, *Munz 9544* (C, Po); 53 mi. S.E. of Tecate, *Peirson 5863* (CAS, CI); San Pedro Martir, *Robertson 34* (C), May 27, 1893, *Brandege* (C), *Goldman 1213* (Ph, US).

The distinctions pointed out by Munz and Johnston to separate their variety from *P. linarioides* included the extreme western range, the broader oblanceolate leaves up to 2.5 mm wide and not more than 15 mm long, and

the very weak beard on the lower lip of the narrower corolla. These may be supplemented by the fact that the corolla is not only less inflated than in *P. linarioides* and apparently lacks the prominent guide lines into the throat which mark that species, but its average dimensions are in every way smaller.

Coupled with the morphological distinctions is the fact that *P. californicus* is separated from *P. linarioides* by a geographic hiatus of more than 300 miles (480 km) with a formidable desert between them. Accordingly, it would appear justifiable to conclude that the two are distinct ecospecies at present although their common origin is scarcely open to doubt.

*Penstemon californicus* has most in common with *P. linarioides* subsp. *compactifolius* of the Flagstaff region, rather than with the forms of southeastern Arizona. Features of habit, the woody base, anthocyanous lower portions of the vegetative shoots, and the thickened leaves, with their peculiar and unevenly distributed pubescence, connect *P. californicus* closely with *P. discolor*, but the two have very different corollas.

#### 10. *Penstemon discolor* Keck, sp. nov.

Fruticulus 2-3 dm altus, multicaulis; caulibus e basi decumbente nigrescente et lignescente erectis pallescentibus cinereo-puberulis; foliis 5-10 mm longis confertis angustissime lineari-oblongatis compresso-clavatis mucronatis integerrimis subtus convexis glaberrimis viridibus supra planis dealbatis minute adpresso-puberulis, basi minute ciliolatis, floralibus gradatim in bracteas subulatas breves diminutis; racemo paucifloro virgato undique viscido 2-6 cm longo; pedunculis adpressis 1-floris brevissimis; sepalis 3.5-5 mm longis ovato-lanceolatis acuminatis margine subscariosis integris; corollis ut videtur albescenti-lilacinis dilatato-infundibuliformibus plerisque 10 mm longis, palato barbato, limbo breviter bilabiato, lobis brevibus subaequalibus; loculis antherarum laxae divaricatis anguste oblongis 0.8 mm longis glabris; filamentis sterili longitudinaliter longe barbato; capsula 4.5 mm longa.

Type: *Forrest Shreve no. 5319* (University of California Herbarium, no. 277189), collected in Bear Canyon, Santa Catalina Mts., Pima County, Arizona, at 7,000 feet (2,135 m) elevation, June 30, 1917; isotypes GH, US, and Desert Laboratory of Carnegie Institution, Tucson, Arizona.

The only other collections seen of this species are: Bear Canyon, 6,100 ft. (1,860 m) elevation, *Shreve 5311* (US); rim of Bear Canyon, *Thorner 7175* (UAriz).

This well marked species of very local distribution differs from its nearest relative, *P. linarioides* Gray, which occurs in the mountains farther east in Arizona, in its small, pale corollas, in its short, divaricate,

bicolored, fleshy leaves, in its extensive decumbent woody base and short internodes, and, to a less extent, in its less scarious sepals and more glandular inflorescence.

### Subsection 3. *Laricifolii*, new subsection

Plants essentially glabrous throughout; flowering stems erect from the closely crowded compact foliaceous rosettes that surmount the branching lignescent root-crown and form a cushion-plant; leaves filiform; corolla not viscid, tubular-campanulate, with prominent regular spreading limb. Monotypic.

#### 11. *PENSTEMON LARICIFOLIUS* Hook. et Arn.

*Penstemon laricifolius* Hook. et Arn., Bot. Beech. Suppl. 376. 1840.

Lignescent caudex subterranean, multibranched; flowering stems 10–20 (–25) cm tall, arising from dense leafy rosettes, glabrous or finely puberulent; leaves filiform, rarely wider, 15–35 mm long, uniform throughout; calyx-lobes lance-ovate, abruptly acuminate, glabrous, the margin prominently scarious below,  $\pm$  erosulate; corolla 12–18 mm long, *ca.* 5 mm wide at summit of throat, villous across base of lower lip; anther-sacs lance-oblong; deep; staminode slightly exserted, bearded along the outer third with short flattened yellowish hairs.

#### KEY TO THE SUBSPECIES

- Corolla purple, 15–18 mm long, gradually amplate.....11a. *P. l.* subsp. *typicus*  
 Corolla white tinged with greenish yellow, 12–15 mm long, more abruptly amplate.....  
 .....12b. *P. l.* subsp. *exilifolius*

#### 11a. *Penstemon laricifolius* subsp. *typicus* Keck, nom. nov.

*Penstemon laricifolius* Hook. et Arn., l.c.

*P. exilifolius* var. *desertus* A. Nels., Bull. Torr. Club **28**: 231, 1901. "This variety occurs sparingly on dry sandstone ridges in the Red Desert [Wyoming]. Point of Rocks, June 12, 1900, [A. Nelson] no. 7160."

Hooker and Arnott state, "Hab. Snake Fort, Snake Country, [a friend of] *Mr. Tolmie*." The type in Herb. Hookerianum, Kew, of which I have seen phototypes (C, CI, GH, SU), and isotypes (GH, NY), is unmistakably of the present unit although the species has now been frequently collected in Wyoming but has not been rediscovered in Idaho if, indeed, the type came from within what are now the bounds of that state.

WYOMING. Big Horn Co.: Big Horn Mts., *Ownbey* 830 (CI); Shell Creek Canyon, near Brindle Creek (CI); Indian Rock (RM). Washakie Co.: Lower Ten Sleep Canyon, *Ownbey* 798 (CI). Hot Springs Co.: Owl Creek, *Parry* 206 (F, GH, NY, Ph). Natrona Co.: Bessemer, *Goodding* 181 (GH, M, NY, RM, US); Garfield Peak (RM); Platte River Canyon (M, RM). Fremont Co.: Birds Eye, *Nelson* 9363 (GH, M, NY, RM, SU, US); Camp Stambaugh (US); Wind River Mts., (GH, US). Sublette Co.:

Big Sandy (US); between Eden and Big Piney, *Payson* 2567 (C, GH, M, RM, US); 20 mi. W. of Big Piney (M, RM). Sweetwater Co.: Leucite Hills, *Merrill & Wilcox* 514 (GH, RM, US); 10 mi. E. of Point of Rocks (CI, SU); Point of Rocks, *Nelson* 7160 (RM, type of *P. exilifolius* var. *desertus*; isotypes CM, F, GH, M, NY, US); Table Rock (RM). Carbon Co.: Freezeout Hills, *Payson* 4809 (RM); Saratoga, *Payson* 2532 (C, GH, M, NY, RM, US).

11b. *Penstemon laricifolius* subsp. *exilifolius* (A. Nels.) Keck, comb. nov.

*Penstemon exilifolius* A. Nels., Bull. Torr. Club 28: 230. 1901.

*P. laricifolius* var. *exilifolius* Payson, Univ. Wyo. Publ. Bot. 1: 97. 1924.

In habit identical with subsp. *typicus*; a xerophytic cushion-plant of the rocky plains of Wyoming, extending its range slightly into Colorado. This subspecies occurs southeasterly of subsp. *typicus*, but their ranges apparently overlap to a slight extent. "The latter [A. Nelson 7460] is taken as the type and is from Halleck Cañon, July 6, 1900."

WYOMING. Albany Co.: Rock River, *Macbride* 2782 (RM); Laramie Hills (NY); Laramie Plains, *Nelson* 419 (GH, M, NY, RM, US); Millbrook, *Keck* 904 (C, CI, Kew, Ph, Po, SU); Cummins, *Nelson* 1442 (C, GH, RM, US); Sandcreek Pass (C, RM); Laramie (C, NY, SU); Halleck Canyon, *Nelson* 7460 (RM, type; isotypes CM, GH, M, NY, SU, US); Red Buttes (US); Sheep Mt., *Goodding* 2086 (CM, NY, RM, US); mouth of Woods Creek, *Keck* 903 (Berlin, C, CAS, CI, Copenhagen, GH, Kew, M, Ph, Po, SU). COLORADO. Larimer Co.: Medicine Bow Mts., Aug. 4, 1891, *Crandall* (NY); Cherokee Park, *Johnston & Hedgecock* 432 (GH, NY).

As indicated in the key, these subspecies are morphologically separable by their flowers which differ in length, shape and color. Since the difference in length is not pronounced in much material from central Wyoming, and since the difference in shape is best observed when one has at hand material of both subspecies for comparison, it follows that color of the corolla is the easiest field character to use. Unfortunately this character is not always clear-cut; collections of subsp. *typicus* have been made with pink corollas, not only in the region where the subspecies approach each other, but in Big Horn County. On the other hand, material with purplish flowers has been collected near Laramie (*Nelson* 10701, C, RM), definitely in the midst of subsp. *exilifolius*.

For these reasons, I object to calling the two units distinct species, although I believe they are excellent ecotypes.

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## Fasciation and its relation to problems of growth

### I. Shape changes in the shoot

S. C. BAUSOR

(WITH SIXTEEN FIGURES)

Fasciation is an abnormal condition resulting in the flattening of normally cylindrical structures. The term, as originally used, implied that two or more similar cylindrical organs, chiefly stems, had fused in one plane, thus producing the flattened effect. The term "fasciation" is derived from the Latin, *fascia*, a banding, and was first used in this connection by Olaus Borrich (Moebius, 1927).<sup>1</sup> In terms of symmetry relations it has been described as a phenomenon causing a change from radial to bilateral symmetry, or to structures lacking symmetry.

The degree of fasciation is variable, but in many cases is so extreme as to warrant the name, "riband-fasciation." This is the commonest manifestation of the phenomenon.

Irregularities in distribution of the leaves on the stem invariably accompany fasciation and in some cases an upset in phyllotaxy precedes the actual change in shape. This has led to the category of "cylindrical fasciation" (Blaringhem, 1908; Martin-Sans, 1929), including all cases of disturbance of phyllotaxy, even when fasciation fails to accompany it.

"Ring-fasciation" is still another abnormal condition which sometimes accompanies the riband type, although it too, as in the case of aberrant foliar arrangement, may appear separately. A hollow tubular structure results, which may bear leaves, stems, and flowers internally, as well as externally. In the cases studied in histological detail (deVries, 1892; Nestler, 1894b; Conard, 1901; Knox, 1908; Compton, 1911), it was shown that there is a tissue duplication, the tissues of the inner cylinder being inverted. Ring fasciation, therefore, is an entirely separate state from that of riband fasciation.

Torsion is also a phenomenon which almost invariably accompanies fasciation and which may also exist separately (deVries, 1910). The fortunate choice of the name precludes any confusion with fasciation.

The present work was undertaken in the hope of finally arriving at a solution of the immediate causes of fasciation and of seeking out the morphological and physiological relationships between fasciated and normal growths. In this paper, the first of this series, an attempt is made to describe fasciation quantitatively and to show the relations between the

<sup>1</sup> Editor's note.—Literature cited in this paper will be listed at the end of the second paper of this series, to be published in the October Bulletin.

data obtained by measurement and the cellular composition of normal and fasciated stems. Only fasciation of the riband type will be discussed.

#### LITERATURE REVIEW

*General.* Organic shape must be considered of prime importance among biological phenomena. It represents the organization of the products resulting from growth, and is a *sine qua non* of the very existence of life in all higher forms. D'Arcy Thompson (1917) emphasized the value of interpreting morphological phenomena in physical terms. He pointed out that form is the resultant of rates of growth, and that with increasing size, shape may remain constant or regularly change, depending upon "specific rates of growth in various directions." The guiding principles, among others considered, are surface phenomena tending to produce the minimum area per unit mass, and the physiological limitation inherent in the law of similitude in enlarging structures. Bower, in 1930, published a detailed account of shape changes occurring in vascular tissue, illustrating the correlation between size and shape. His hypothesis rests upon the assumption that contact with living cells is necessary for vascular translocation, which he terms the "vitalization" of the wood. Shape changes occur which increase the surface contact with living elements, resulting in a physiologically tenable system.

Sinnott (since 1922) analysed shape genetically and determined that in *Cucurbita pepo* a single gene, in some cases, or two or more in others, produced definite shapes. Crosses resulted in typical mendelian ratios. It also was shown that while size did affect shape somewhat, the two could be analysed as separate effects. Furthermore, it was shown (1929) that the characteristic shapes were determined very early in the primordium, but that slight, constant changes occurred as the fruit enlarged.

Sinnott and Kaiser (1934) showed that in *Capsicum*, fruit shapes of widely different form are similar as young primordia and that changes occur subsequently, depending upon the changes in the rates of relative growth in length and width.

The cock's comb (*Celosia*) is a familiar example of hereditary fasciation. DeVries (1894, 1899, 1910), White (1916), Hagawari (1926), Kelly (1927), Imai (1930, 1934), et al., have shown that fasciation may be inherited in other forms. DeVries established seven races of fasciated plants, in none of which was he able to get 100 per cent fasciations. Some always appeared normal, although in breeding experiments they resembled fasciated plants. He termed this inheritance "ever-sporting." White isolated mutant races of fasciated *Nicotiana*, in which the abnormalities appeared late in the development of the plants. Breeding experiments indicated a

monofactorial difference between fasciated and normal plants. The fasciations, however, were quite variable in degree and it was at times difficult to segregate the types.

Klebs (1910) emphasized the importance of environment in determining form. His comment, although not with reference to fasciation, probably is applicable. "It is a character of a species that it always exhibits a constant relation to a particular environment."

Vavilov (1922), in his discussion of homologous series in variation, pointed out that fasciation and some other characters, such as albinism, nanism, gigantism, are types of variation which occur generally throughout vascular plants.

The similarity of abnormalities in plants not closely related probably is due to the similarity of organization of the shoot.

Schneck (1905), Sorauer (1909), Brannon (1914), and Kienholz (1932) showed that fasciated woody stems differ histologically from the normal only in shape. Moss (1924) reported two types of variation in the roots of *Caltha*, which he described as fasciated. In the first the cross-sectional outline of the whole structure was elliptical, the vascular tissue being arranged either into an elliptical stele following the outline of the root, or into two circular steles. In the second type the cross-sectional outline of the root was circular while the stele was elliptical.

Nicolas (1928) studied a single fasciated plant of *Chrysanthemum Myconis* in which he found several steles embedded in a ground tissue. In the center of each stele was a cavity bordered by epidermal tissue. Next in order was cortex, endodermis, pericycle, phloem and xylem, so that the tissues were completely inverted and the ground tissue was the common "pith" for the individual steles. This is probably a very exaggerated case of ring fasciation. Küster (1913) mentioned that medullary rays are often abnormally broadened in fasciated plants, but that this character is not peculiar to the abnormality. Blaringhem (1911) considered undulations in fasciated stems as due to increased cell division caused by unequal nourishment.

Nestler (1894a) showed that the apical meristem of certain fasciated plants was flattened and transformed into a vegetative line in forms which normally have a vegetative cone, and that forms which normally have a single apical cell possessed a line of apical cells.

Johansen (1930) described the development of the embryo in a fasciated line of *Clarkia*. He showed that development proceeded with "absence of order, sequence, and direction in the formation of all cell walls except the first transverse partition." Jones (1935), comparing fasciation



with tumor formation, pointed out that both abnormalities result from unregulated growth.

*Experimental production of fasciation by decapitation in Phaseolus multiflorus and some other plants.* In 1859 Julius Sachs, working upon the physiological chemistry and anatomy of *Phaseolus multiflorus*, discovered that by removing the epicotyl in a very early stage of development the buds in the axils of the cotyledons became fasciated upon further growth. Lamarlière (1899) produced fasciations in the secondary axillary shoots of *Barkhausia* by removing the top of the plants and the first formed axillary shoots. He suggested that abnormal buds were formed as the result of pressure in the crowded leaf axil.

Goebel (1900) emphasized the importance of Sachs' experimental production of fasciation and mentioned that *Vicia faba* seedlings reacted in the same way. He suggested that a sudden rush of sap into the buds caused the abnormality. Lopriore (1904a) again investigated the problem of the production of fasciation in *Phaseolus* and confirmed Sachs, but denied that *Vicia faba* produced fasciation under these conditions. He also showed (1904b) that fasciated roots could be produced by removing the hypocotyl. Blaringhem (1908) reported that in a great many plants fasciation and other anomalies appeared after mutilations.

In 1912, Reed published a short account of axillary fasciations, stating that they readily occurred in *P. multiflorus*, and to a smaller degree in *Vicia faba* and *Pisum sativum*. On the other hand, seedlings with epigyeal cotyledons did not fasciate under the same conditions, as for example, *Phaseolus vulgaris*, *Lupinus Douglassii*, *Ricinus communis*, and *Cucurbita pepo*.

Bouygues (1925) took up the study again and discovered that, contrary to Sachs' opinion, the time at which the epicotyl of *P. multiflorus* is cut is not an important factor. He mentioned that fasciation did not occur under the same conditions in *Ervum lens*, *Pisum sativum*, *Vicia faba* and *Aesculus hippocastanum*.

Georgescu (1925) produced similar axillary fasciations in *Quercus* seedlings. At a later date (1927) he dealt extensively with fasciation in decapitated seedlings of *P. multiflorus*, and found that it varied from 20 to 87 per cent in different cultures. He experimentally demonstrated that the phenomenon was quite independent of external conditions.

It is evident that mutilations produce structural anomalies; that some plants, like *Phaseolus multiflorus*, react very readily, while others, such as *Vicia faba* and *Pisum sativum*, for example, do so to a lesser degree. Many plants, however, cannot be induced to fasciate under the same ex-

perimental conditions, although, as in *Cucurbita pepo*, mature individuals have been found fasciated in the field (Tadulingam, 1925).

#### METHODS AND MATERIALS

*Phaseolus multiflorus*, Willd. variety *English Scarlet Runner*, was used for this study.

The method for producing fasciation was, with a few modifications, similar to that of previous workers. The seeds were sown vertically, with the micropylar end downward, so as to produce a straight root. When the plants were about a week old they were transplanted in such a way as to leave the cotyledons above the level of the soil, and the epicotyls were cut off with a razor about two centimeters from the cotyledonary node. The axillary buds at the cotyledonary node made rapid growth and in about two weeks were well developed and ready for analysis.

Two diameter measurements were made with a vernier caliper at successive positions along the axis of the axillary shoots. The first two measurements were in the center of the first internode, one in the plane of leaf insertion of the node above, and the second at right angles to it. At the first node, two measurements were taken, one in the plane of leaf attachment, and the other at right angles to it. The next two measurements, made in the second internode, directly above the first node, were similarly taken with reference to the leaf at the first node. The fourth and fifth pairs of measurements were respectively at the second node, and in the third internode, directly above that node. These measurements, however, were taken with reference to the second leaf. The sixth and seventh pairs of measurements were similarly recorded at the third node, and in the fourth internode directly above it, this time with reference to the attachment of the third leaf, and so on to the apex of the shoot. The internodal measurements, with the exception of the first, were all taken immediately above the preceding node, the first measurement in the plane of leaf insertion and the second at right angles to it.

Measuring the shoot as described above, the shapes of the nodes are morphologically comparable, as are also the internodes, although actual points of measurement are in a spiral following the leaf arrangement. In this way it is possible to consider the shape of the nodes and internodes as if they were superposed one above the other. Thus, Node 1 can be compared with Nodes 2 and 3, Node 2 with Nodes 1 and 3, etc. The internode measurements also are comparable, the whole system being based on the position of the leaf.

The quotient obtained by dividing the first measurement by the meas-

urement at right angles to it was used to express shape in quantitative terms, as a shape index.

For histological studies both free-hand and microtome sections were employed. Drawings or photographs of the shoots were made for reference before sectioning.

Fixations were made in 70% alcohol, formo-acetic-alcohol, and in Allen and Wilson's modification of Bouin's solution, the last being the most satisfactory.

Serial transverse and longitudinal sections were made at 10, 15, and 20 microns, and stained with safranin and light green, or safranin and gentian violet.

I wish to thank Professor C. C. Curtis, under whom this work was begun, for inspiring encouragement in pursuing the subject and for his patient criticism of the work. Also, I wish to thank Professor E. W. Sinnott, Professor E. B. Matzke, and other members of the Department of Botany at Columbia University for helpful criticism.

#### THE NATURE OF THE AXILLARY SHOOT AND ITS VARIATIONS

Usually one bud develops in the axil of each cotyledon, either as a normal or fasciated shoot (fig. A). The development of one shoot is apparently independent of the other, and plants are found with two normal, one normal and one fasciated, or two fasciated branches. Sometimes several secondary buds develop, which may also be fasciated or normal, with no systematic regularity (fig. B). The first leaf may be uni-foliate as are the juvenile leaves of the epicotyl, or it may be tri-foliate.

Associated with fasciation are torsions and bending often causing the stem to split, and foliar abnormalities. The petiole is not uncommonly fasciated (fig. C), in which case it usually has an increased number of leaflets. Among other foliar derangements are leaves with but two leaflets, apparently the result of a fusion of the apical leaflet with one of the laterals, the resulting structure often having two apices. Again one or both lateral leaflets may be suppressed and their corresponding stipels developed into a characteristic luna-shaped lamina, with a strong vein on the outer margin ending in a point. The stipules are often displaced, and being stretched by the elongating internode, appear as thin irregular membranes vertically or obliquely placed on the stem.

#### CHANGES IN THE SHAPE OF THE SHOOT

Both normal and fasciated shoots were measured and the ratio of diameters used as a shape index, as described above. In this way it was possible to compare the shapes and the changes in shape of the shoots, and to arrive at an expression of fasciation in quantitative terms.

*The normal shoot.* Analysis of measurements made at the nodes and internodes of normal axillary shoots brought to light the fact that the normal stem was not a cylindrical nor a conical structure from base to apex, but that its shape varied periodically. At the internodes it tended to be cylindrical, while at the nodes it deviated from the shape index of 1.00, which represents a circular outline. At the node the diameter in the plane of leaf insertion invariably increased more than the diameter at right angles to it. Thus, in Plant 25, taken as an example of extreme divergence, the



Figs. A-C. A. Decapitated seedling of *Phaseolus multiflorus* with one fasciated and one normal axillary shoot. B. Decapitated seedling in which several axillary buds developed, one of which was fasciated. C. Decapitated seedling with two fasciated axillary shoots, one having an abnormal leaf with fasciated petiole. Splitting occurs in both shoots.

first node has an index of 2.05, which indicates that the diameter in the plane of leaf insertion is over twice that at right angles to it. Similarly, in plant 9, the index at the first node is 1.18, at the second node 1.50, and 1.20 at the third. In Plant 28, the first node had an index of 1.00, the second node 1.13. The first node of this plant was represented only by stipules and the second by a small leaf. In Plant 26 the first significant departure from cylindrical occurred at the third node, the index of which jumped suddenly to 1.56. The first two nodes had poorly developed leaves. These changes are undoubtedly correlated with the presence of the leaf, since the points at which the shape varies from cylindrical are at the nodes. Therefore, this variation will hereafter be referred to in this work as the *nodal effect*.

The nodal effect apparently is dependent upon the growth and development of the leaf.

The internodal indices fluctuate around 1.00. Extremes of internodal variation are shown in Plants 1 and 25: at the second internode of Plant 1 the shape index is 1.20, while for Plant 25 it is 0.77. In a frequency distribution of 143 internodes, 48% (68) fell within the index range 1.03 to 0.97; 17% (24) fell within 1.03 to 1.06, and 0.97 to 0.94; 17% (24) were in the 1.06 to 1.09, and 0.94 to 0.91 groups; 10% (15) fell within 1.09 to 1.12, and 0.91 to 0.88. The remaining 8% (12) diverged still further from cylindrical.

Since the internodal measurements, except the first, were made directly above the nodes, it appears that the leaf has but little effect upon the stem above the point of leaf insertion. Thus, in Plants 4 and 5 the nodal effect at the second node is 1.55 and 1.52 respectively, while the internodal indices directly above are 1.09 and 0.95.

For the above study the shape indices from base to apex of 34 normal axillary shoots were determined. The total number of nodes and internodes analysed were 127 and 143 respectively. The following indices and measurements illustrate the shape-changes that the shoot of *Phaseolus multiflorus* undergoes in normal development.<sup>2</sup>

Measurements and consequent shape indices for:

Plant 1—First internode,  $3.1 \times 3.4$  mm., shape index 1.09; first node,  $3.3 \times 4.4$  mm., shape index 1.33; second internode,  $2.0 \times 2.4$  mm., shape index 1.20; second node,  $2.8 \times 3.6$ , shape index 1.28; third internode,  $2.0 \times 2.0$  mm., shape index 1.00; third node,  $2.3 \times 2.6$  mm., shape index 1.13; fourth internode,  $1.7 \times 1.7$  mm., shape index 1.00; fourth node  $1.6 \times 1.6$  mm., shape index 1.00; fifth internode  $1.2 \times 1.2$  mm., shape index 1.00.

In the following five additional examples the dimensions are given in millimeters and the shape index shown in parenthesis. The first figures are for the first internode and the following figures for the first node, second internode, second node, etc., to the apex of the shoot.

Plant 2— $2.8 \times 2.8$  (1.00);  $3.0 \times 4.2$  (1.40);  $2.5 \times 2.7$  (1.08);  $2.5 \times 3.3$  (1.32);  $2.0 \times 2.0$  (1.00);  $2.3 \times 2.9$  (1.26);  $1.6 \times 1.8$  (1.12).

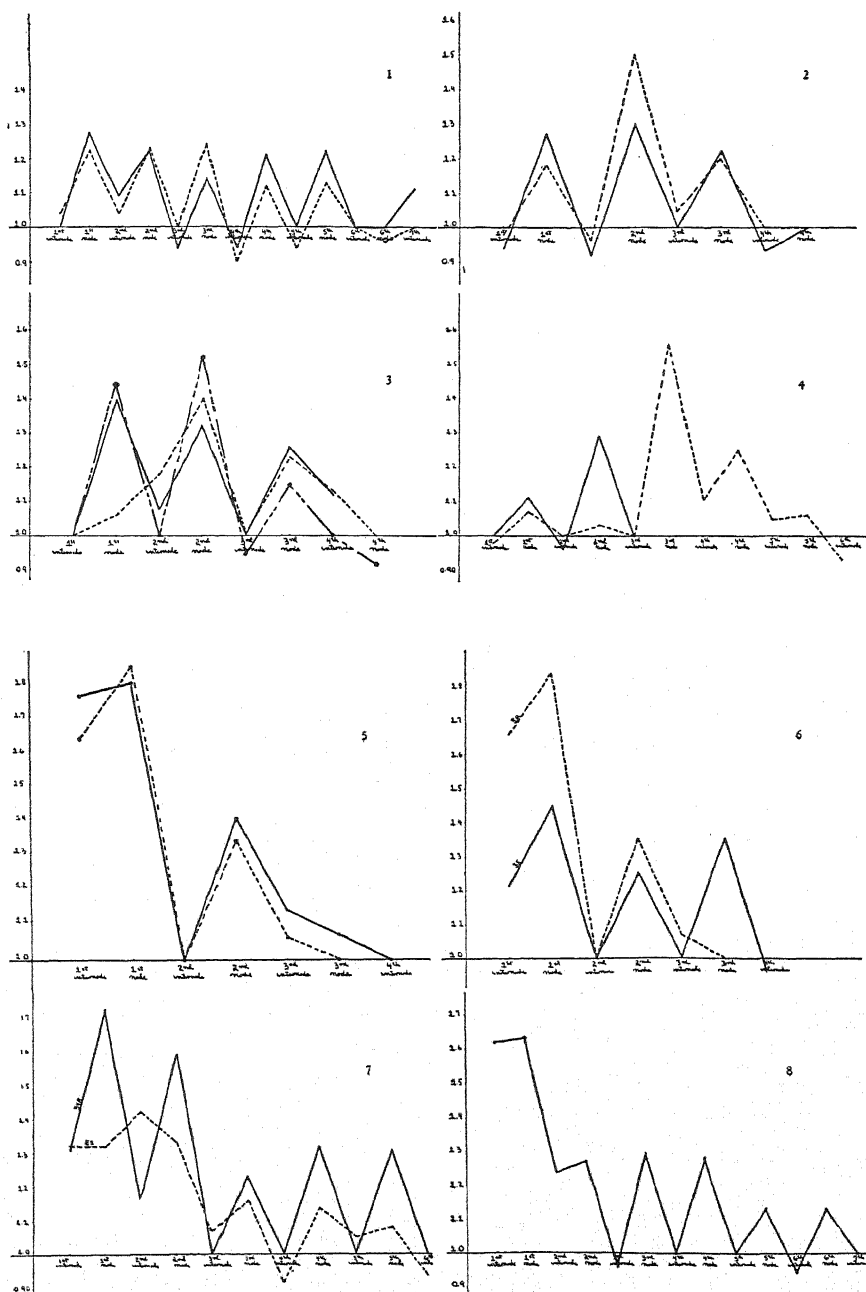
Plant 5— $2.8 \times 2.8$  (1.00);  $3.2 \times 4.5$  (1.44);  $2.3 \times 2.3$  (1.00);  $2.3 \times 3.5$  (1.52);  $2.0 \times 1.9$  (0.95);  $2.0 \times 2.3$  (1.15);  $1.7 \times 1.7$  (1.00);  $1.3 \times 1.2$  (0.92).

Plant 13— $2.8 \times 2.4$  (0.86);  $3.0 \times 3.4$  (1.13);  $2.2 \times 2.0$  (0.90);  $2.3 \times 2.7$  (1.17);  $1.8 \times 1.6$  (0.90);  $1.5 \times 1.4$  (0.93);  $1.4 \times 1.3$  (0.93).

Plant 17— $2.9 \times 3.4$  (1.17);  $2.9 \times 4.2$  (1.45);  $2.5 \times 2.7$  (1.08);  $2.7 \times 4.4$  (1.63);  $1.9 \times 1.9$  (1.00);  $1.7 \times 1.7$  (1.00);  $1.4 \times 1.4$  (1.00).

Plant 32— $3.4 \times 3.3$  (0.97);  $3.6 \times 5.5$  (1.53);  $2.8 \times 3.1$  (1.10);  $3.0 \times 4.0$  (1.33);  $2.5 \times 2.3$  (0.92).

<sup>2</sup> Space does not permit the recording of the complete table.



Graphs 1-8; explanation in the text.

From these few citations it is clear that the leaf greatly influences the magnitude, but more especially the shape of the shoot.

The nodal effect and the immediate return to a nearly cylindrical form can be seen more clearly in a graph. Graphs 1 to 4 show plottings of shape indices against the position on the stem, i.e., at the nodes and internodes at which the measurements were taken. The abscissa represents the index 1.00, or cylindrical form. It can be seen that there is a periodicity of shape changes in the normal axillary stem. The change caused by the nodal effect is always in the same direction—greater than unity—while at the internodes the shape fluctuates about 1.00.

*The fasciated shoot.* Measurements and shape indices of 47 fasciated axillary shoots were determined in the same way as those of the normal shoots. 215 internodes and 182 nodes were analysed.

As in the normal shoots there is a periodic shape change associated with foliar development. The shape of the internodes, however, presents the main difference between normal and fasciated development. The internodal indices are considerably greater than unity, while at the nodes the divergences are usually still greater, resulting from a combined action of fasciation and nodal effect.

In all cases the fasciated shoots eventually become normal. The restoration to normal is very sudden. In Plant 3, for example, the third internode index is 1.85, the third node 1.43, and immediately above, in the fourth internode, it is 1.05. In Plant 38, the first internode shape is 1.95 and in the second internode it is 1.00. In Plant 46, the first internode is 1.64, the first node 1.83, and immediately above it, in the second internode, the index abruptly becomes 1.00. The shoot may return to normal at the second, third, fourth, or fifth internodes. Only rarely does the fasciated state persist beyond this point.

The following measurements and indices show the nature of the fasciated shoot:

Dimensions are in millimeters and the shape index is in parenthesis. The first figures are those taken at the first internode, the second, those of the first node, etc., to the apex of the shoot.

Plant 2— $3.5 \times 5.5$  (1.57);  $3.5 \times 6.4$  (1.83);  $3.3 \times 4.0$  (1.21);  $3.0 \times 4.3$  (1.43);  $2.5 \times 3.0$  (1.20);  $2.7 \times 4.1$  (1.52);  $2.9 \times 3.3$  (1.14);  $3.4 \times 3.4$  (1.00);  $2.4 \times 2.3$  (0.96);  $2.2 \times 2.3$  (1.05);  $1.7 \times 1.6$  (0.94);  $1.5 \times 1.4$  (0.93);  $1.3 \times 1.2$  (0.92).

Plant 4— $3.3 \times 3.3$  (1.00);  $3.5 \times 4.0$  (1.14);  $2.6 \times 3.7$  (1.43);  $2.6 \times 3.7$  (1.43);  $1.9 \times 2.3$  (1.21);  $2.1 \times 2.8$  (1.33);  $1.9 \times 1.9$  (1.00);  $1.7 \times 1.6$  (0.94);  $1.2 \times 1.2$  (1.00).

- Plant 21— $3.3 \times 4.4$  (1.33);  $3.4 \times 4.7$  (1.38);  $2.7 \times 3.4$  (1.26);  $2.7 \times 4.0$  (1.48);  $2.2 \times 2.3$  (1.05);  $2.0 \times 2.4$  (1.20);  $1.6 \times 1.6$  (1.00);  $1.5 \times 1.5$  (1.00);  $1.2 \times 1.1$  (0.92).
- Plant 28— $2.9 \times 3.8$  (1.31);  $2.9 \times 5.0$  (1.72);  $2.5 \times 2.9$  (1.16);  $2.7 \times 4.3$  (1.59);  $2.3 \times 2.3$  (1.00);  $3.0 \times 3.7$  (1.23);  $1.9 \times 1.9$  (1.00);  $2.8 \times 3.7$  (1.32);  $1.7 \times 1.7$  (1.00);  $2.5 \times 2.8$  (1.12);  $1.6 \times 1.6$  (1.00).
- Plant 29— $2.8 \times 4.7$  (1.68);  $3.0 \times 4.9$  (1.63);  $2.7 \times 2.3$  (0.85);  $2.3 \times 2.6$  (1.13);  $1.5 \times 1.5$  (1.00);  $1.5 \times 1.5$  (1.00).
- Plant 31— $3.9 \times 5.5$  (1.41);  $3.8 \times 6.0$  (1.58);  $3.5 \times 5.9$  (1.64);  $2.6 \times 5.4$  (2.08);  $2.3 \times 2.5$  (1.10);  $2.3 \times 3.8$  (1.65);  $1.6 \times 2.0$  (1.25);  $1.6 \times 2.1$  (1.31);  $1.4 \times 1.4$  (1.00).
- Plant 42— $3.3 \times 4.2$  (1.27);  $3.3 \times 4.5$  (1.36);  $2.6 \times 2.6$  (1.00);  $2.7 \times 3.6$  (1.33);  $2.2 \times 2.0$  (0.91);  $2.1 \times 2.5$  (1.19);  $1.4 \times 1.2$  (0.86).
- Plant 43— $2.7 \times 4.0$  (1.48);  $2.6 \times 4.5$  (1.73);  $2.1 \times 2.3$  (1.10);  $2.6 \times 2.8$  (1.08);  $1.9 \times 1.7$  (0.89);  $2.2 \times 2.3$  (1.05);  $1.9 \times 1.7$  (0.89);  $2.4 \times 3.0$  (1.25);  $1.7 \times 1.5$  (0.88);  $2.3 \times 2.2$  (0.96);  $1.5 \times 1.4$  (0.93);  $2.1 \times 2.3$  (1.10);  $1.4 \times 1.3$  (0.93).
- Plant 47— $2.9 \times 5.1$  (1.76);  $3.0 \times 5.4$  (1.80);  $2.0 \times 2.2$  (1.10);  $2.0 \times 2.8$  (1.40);  $1.5 \times 1.7$  (1.13);  $1.5 \times 1.6$  (1.07);  $1.3 \times 1.3$  (1.00).

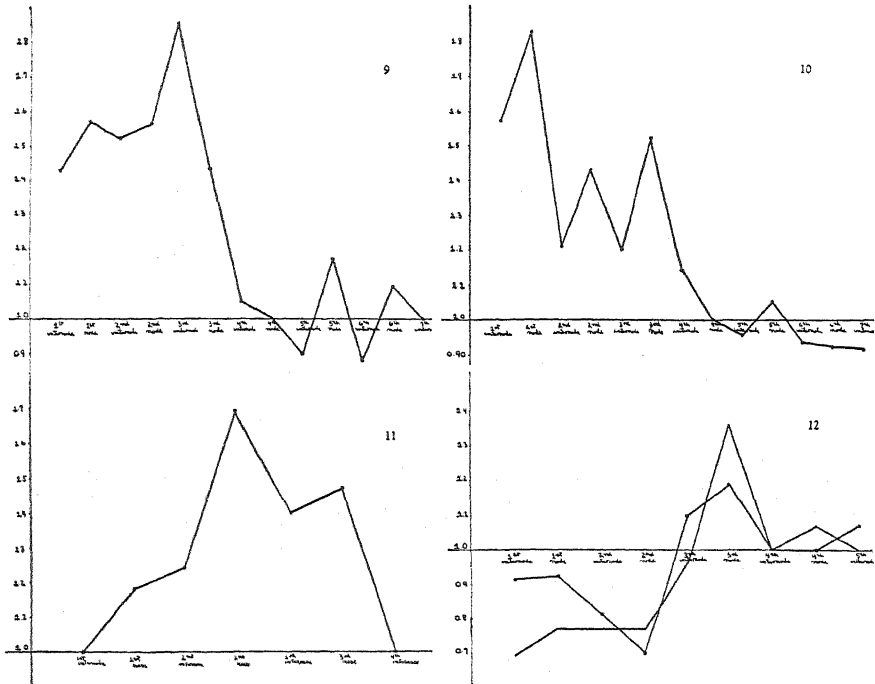
The relation of nodes to internodes, and the course of the changes taking place in the fasciated stem are more clearly shown in Graphs 5-12. As in the series of normal graphs, the ordinates represent the shape indices and the abscissas the positions along the stem from base to apex. In Graphs 5 and 6 four plants are shown which return to normal very abruptly at the second internode. The distance of the points from the abscissa represents the degree of fasciation. At the first node the combined nodal effect and fasciation are seen in a rise in the shape indices. At the second internode the stems are cylindrical. Above this point the graphs are similar to those of normal axillary shoots.

In Graphs 7 and 8 three plants are shown which become normal at the third internode. There are two sudden changes here. The first change occurs at the second internode abruptly as before, but although diminished, the shape index is still far from unity. The second change brings the stem abruptly to normal cylindrical form. In E1, the first leaf was so close to the base of the plant that only a single measurement for the first internode and the first node was possible. This plant becomes more fasciated at the second internode, and the index at this point is larger than that of the first or the second node. The third node brings the stem to normal.

Graphs 9 and 10 illustrate plants returning to normal at the fourth internode. In Graph 9 there is a progressive increase in the degree of fasciation, which reaches its high point in the third internode. The fourth



internode suddenly becomes normal again. In Graph 10 the greatest degree of fasciation appears at the base of the plant, and it is steadily decreased by abrupt stages until it is definitely normal with the fourth node. At the second and third internodes the shape is on the outskirts of the extreme of a normal shape frequency-distribution, while the index of the fourth internode overlaps the 5% class. Abrupt rises occur at the first, second, and third nodes, indicating nodal effect.



Graphs 9-12; explanation in the text.

In Graph 11 the base of the plant is normal, becomes fasciated at the second internode and abruptly returns at the fourth. The point of greatest fasciation is the third internode.

In Graph 12 two plants are shown, the first leaves of which were at right angles to the plane of flattening of the fasciated stem. The indices are therefore negative. The nodal effect in these cases tends to diminish the shape index, since the leaf is located on the flat side of the stem.

From the above data it will be seen that the normal internode is more or less circular in outline, while the fasciated internode is a flattened structure. The absolute shape of the shoot, however, is not an indicator of fasciation, since the shape index at the nodes of the normal stem often

exceeds the quantitative measurements of fasciation. Shape changes due to nodal effect, are, however, histologically different from those of fasciation. Certain cellular features are inherent in such modifications of form, both in the normal and the fasciated stem.

#### HISTOLOGY OF THE NORMAL AND FASCIATED SHOOTS

*The internode.* Although circular in general aspect, the outline of the normal stem is modified by slight ridges which give to it an undulating appearance. These ridges are produced by local enlargement of the cells of the cortex and also by an increase in the number of cells of the pericycle. Slight elevations are produced also by the arching of the epidermal cells

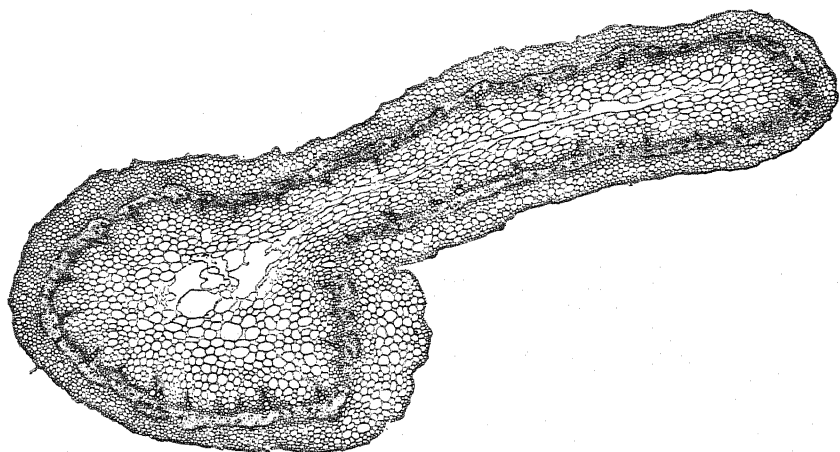


Fig. 13. Cross-section of a fasciated internode showing continuity of tissues. The adaxial end is to the left; it is much better developed than the abaxial sector.

at the stomata. This probably is more pronounced on the petiole than on the internodal stem. The cortical cells are surrounded at the periphery by a single layer of epidermis and internally by a single layer of endodermis. The endodermal tissue differs from the adjacent layer of cortical cells particularly in lacking air spaces on the radial walls, thus forming a completely closed cylinder. A layer of bast fibers lies directly within the endodermis. In older stems these fibers form an almost complete ring, being discontinuous especially in positions between the bundles. Within are several layers of pericycle parenchyma. The phloem regions occur opposite the xylem, but groups also are present unassociated with the wood. These phloem groups are separated from the pith by a complete cylinder of fibers of two or three cell layers, which are compactly arranged,

with almost no air spaces. The cells of this cylinder which lie opposite the protoxylem bundles differentiate as metaxylem elements rather than fibers. Some metaxylem also develops in this tissue independently of the protoxylem.

The primary bundles consist of very small spirally thickened protoxylem and larger pitted metaxylem nearer the fiber ring. At a very early stage the innermost vessels are crushed and become functionless. The parenchyma cells surrounding the protoxylem are smaller than the other pith cells in the same radius. The pith in the center of the stem disintegrates as the stem enlarges. Upon further development a cambium forms outside of the fiber ring and between xylem and phloem.

Figure 13 represents a fasciated stem in cross-section. The organization of the fasciated stem is the same as that just described for the normal, comparing tissue with tissue. The differences are chiefly those of shape. Just as the fasciated stem as a whole differs from the cylindrical in shape, so the individual tissues differ. The epidermis, cortex, endodermis, pericycle, vascular tissues, and pith conform in outline to the general shape of the stem. The tissues, therefore, may be spoken of individually as fasciated tissues.

The shape of the fasciated stem may be elliptical or nearly bilateral. The latter case predominates, the adaxial sector of the branch developing more than the rest. It usually rounds off, as shown in figure 13.

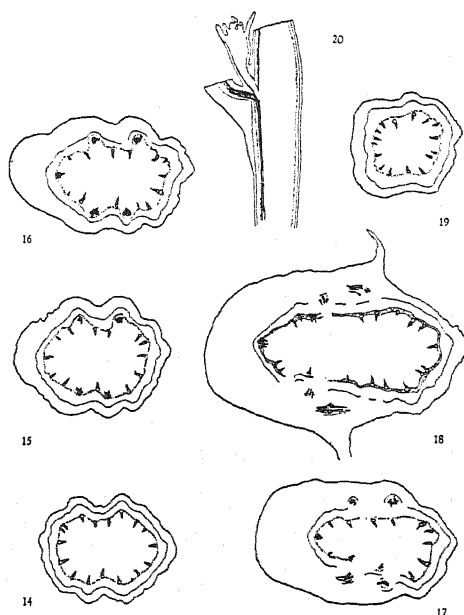
*The nodes.* Analysed quantitatively normal nodes and fasciated internodes are quite similar. The histology of the normal node, however, is quite different from that of the fasciated internode.

Shape changes occurring at the normal node are one-sided, i.e., at the side to which the leaf is attached. The cortical cells in this sector progressively increase in size, reaching maximum development at the place where the leaf diverges from the stem. This enlargement occurs even before the leaf traces separate from the stele (figs. 14, 15, 16, 20). Near the node, the differentiation of leaf traces in this enlarging tissue sector also contributes to the increase in size (figs. 17, 18). Immediately above the node the cortex is slightly larger in the plane of leaf insertion than elsewhere, but the enlargement disappears very quickly above the axillary bud (figs. 19, 20). This explains the nodal effect described in the tables and graphs of normal shape change.

Similar developmental changes take place at the nodes of fasciated shoots. Figures 21-24 and 25-34 are drawings of cross-sections through nodal regions. In figures 21-24 the leaf was located in the plane of the larger diameter. The nodal effect, therefore, tended to further flatten the stem, or to increase the size of its shape index. In figures 25-34 the leaf

was produced in the plane of the shorter axis, which tended to round off the stem and decrease the shape index.

Thus, it is evident that the changes due to nodal effect are the same in normal and fasciated stems; consisting, first, of cortical enlargement, and later combined with the development of leaf traces.



(In figs. 14-34, stiplings represent fiber ring, line outside of it, the endodermis.)

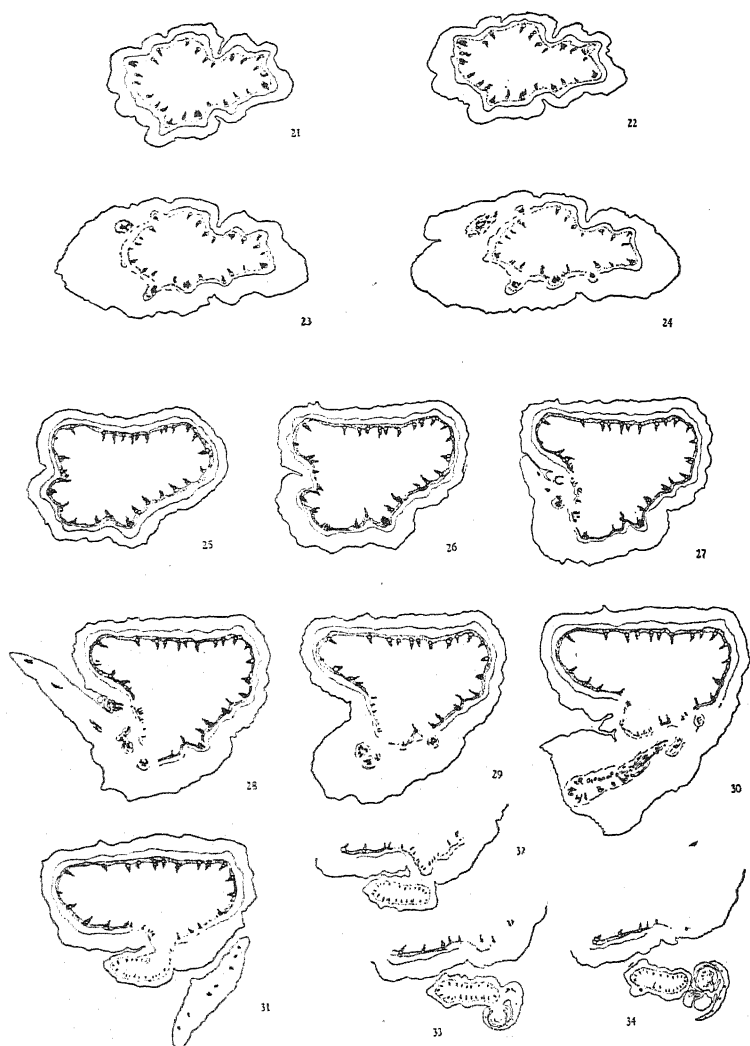
Figs. 14-19. Serial cross-sections through the region of a node of a normal axillary shoot: (14) at internode; (15, 16, 17, 18) progressive enlargement of the cortex on the sector to which leaf is attached; (19) immediately above the node; slight nodal effect still present.

Fig. 20. Longitudinal section, showing: cortical enlargement (at left) progressively increasing toward the node. Immediately above the axillary bud the nodal effect is still in evidence but disappears abruptly.

#### RETURN TO CYLINDRICAL

Although measurements did not show any nodal effect above the leaf in the normal stem, histological analysis indicated that there was a slight, transitory effect in that region. This is illustrated in figure 20, which is a longitudinal section through the nodal region. The extent of the influence of the nodal effect upon the region above was small and was manifest as an enlarged cortical development similar to that below the leaf. That

it was not revealed by caliper readings was due to the fact that the effect was produced only very close to the node.



Figs. 21-24. Serial cross-sections through a node of a fasciated stem in which the leaf was borne along the longer diameter of the stem: (21, 22) cortical enlargement (to the left); (23, 24) further enlargement as the leaf traces leave the stele.

Figs. 25-34. Serial cross-sections through a node of a fasciated stem in which the leaf was borne along the shorter diameter of the stem: (25, 26, 27) cortical enlargement (lower side of figures). In fig. 27 the shape is almost isodiametric. (28, 29, 30) The leaf diverging; (31) cortical enlargement in region of axillary bud; (32, 33, 34) above the node, the cortex is only slightly affected. The axillary bud is fasciated.

Above this region the cortex was uniformly developed and the stem was again cylindrical. In the fasciated shoot changes which restored the cylindrical structures were more complex.

There are two general ways in which the fasciated condition is lost. The fasciated stem may bifurcate, producing two stems, of which both may be normal, or both fasciated, or one may be normal and the other fasciated. However it occurs, the degree of fasciation (shape index) is lessened.

In the second general type, sectors of the original fasciated stem become organized as determinate structures (leaves) which reduce the original fasciation. It is a very common occurrence to find a large fasciated petiole ending the fasciated state of the shoot.

#### DISCUSSION AND CONCLUSIONS

Fasciation in the axillary shoots of *P. multiflorus* is a continuous variation which at times is difficult to distinguish from normal, especially in those indices of shape ranging from 1.20 to 0.85. At the other extreme, one diameter may be more than twice that at right angles to it, and fasciation is quite evident. As has been shown, the chief difference between normal and fasciated growth is one of shape. The tissues of both are similarly differentiated and have identical tissue relations. In fasciated growth the tissues themselves can be distinguished by their shape, like the organ as a whole, and they can be spoken of individually as fasciated.

The shape of the normal stem is periodically changing, varying from a cylindrical form under the influence of the developing leaf. The resulting structure is a cylinder, which becomes elliptical in outline toward the node and which, immediately above, again resumes cylindrical shape. While a given numerical ratio may indicate fasciation, especially if the flattening is considerable, only measurements taken at the internodes are significant. For although a given shape index may indicate fasciation, that same ratio, if it apply to the node of a normal stem, only indicates the enlargement associated with leaf production; or if it apply to the node of a fasciated stem, indicates a combination of nodal effect and fasciation.

The shape indices of normal nodes and fasciated internodes are of different biological value. In the latter, the flattened outline is caused by a general growth increment, greater in one direction than the other, in which differentiation follows as normally in any particular sector. The number of structural differentiations, however, are increased as is shown most obviously in the vascular tissue. In the normal node the shape is changed by a local growth increment, especially in the cortical tissues directly below the node and extended part way around the stem. There also

is a slight cortical enlargement directly above the node, in the same plane, which disappears shortly. Thus, while the shape indices of normal nodes and fasciated internodes may be the same, the factors regulating them are different. The term "nodal effect" is used to distinguish between flattening associated with foliar development, and fasciation.

Nodal effect is independent of the phenomenon of fasciation for it is operative in the fasciated stem as in the normal.

The correlation between the development of the leaf and nodal effect has not been studied but recent work on auxins (Avery, 1935) suggests that materials translocated from the leaf, principally in a downward direction, might influence the development of tissues in their path. The cortex, in particular, is affected, especially nearer the node, less so farther away. The effect above the node is very small and the stem soon becomes cylindrical.

There is a similar tendency for the fasciated stem to assume the cylindrical form, as can be seen by the readiness with which the fasciated shoot returns to normal.

The relation of cell size and number to growth in normal and fasciated stems and to regions of local growth will be discussed in a report of further studies.

#### SUMMARY

1. Fasciation, which was produced in the cotyledonary, axillary shoots of *Phaseolus multiflorus* by the removal of the epicotyl, was studied quantitatively and compared with similar normal shoots.

2. Normal shoots showed periodic axial shape changes correlated with foliar development ("nodal effect").

3. Shape changes due to nodal effect were mainly the result of increased cortical development.

4. Fasciation resulted from a general increase in growth, greater in one direction than in the other.

5. Shape indices cannot be used alone as an indication of fasciation, since the index of nodal effect in normal stems is often equivalent to the index of fasciation.

6. Nodal effect is independent of fasciation and is found in both normal and fasciated stems.

7. Histological comparison of normal and fasciated growth showed that the chief difference between them was that of shape. The relation of tissue to tissue was the same in both.

8. Tissues of fasciated stems differ from those of normal stems as the normal organ as a whole differs from the fasciated.

## Notes on the botanical components of curare

B. A. KRUKOFF AND A. C. SMITH

The present paper is planned to list the botanical components of curare, the arrow poison, as it is prepared by the Tecuna and Java Indians of Amazonia, and to describe native methods of curare preparation. One of the objects of the first author's Sixth Expedition to Brazilian Amazonia was to secure crude material of plants used by Indians in the preparation of this poison, particularly of those plants which contain the active paralyzing principle. The physiological action of this principle is well known; the botanical source of it, at least as regards Brazilian curare, has been in doubt up to the present. During 1935 and 1936 there were made from Brazil by the first author several shipments which contained authentic crude material backed by herbarium specimens. This material is now under thorough chemical and pharmacological study by Merck & Co. Inc. of New York. Authentic wood samples of *Strychnos* spp. have been turned over to Dr. R. A. Cockrell, who has consented to work on the wood anatomy of species of *Strychnos*. Botanical specimens representing the species mentioned in this paper have been deposited in the herbarium of the New York Botanical Garden. Various specialists have kindly made determinations for us in certain families, and we take this opportunity to thank Prof. R. E. Fries (Annonaceae), Mr. N. Y. Sandwith (*Strychnos*), and Dr. O. C. Schmidt (*Aristolochia*).

### CURARE OF THE TECUNAS

Tecuna Indians now occupy the territory drained by some of the northern tributaries of the upper Solimoes. They seldom make use of curare and blow-guns, since having been pacified by Brazilians. The younger generation is not familiar with curare and it was only with difficulty that one very old Indian was found who still accurately remembered the plants entering curare and the method of preparation of the poison so often used by Tecunas in the old days. The description of the preparation of the poison given below is an accurate account of a method used by this old Indian, supplemented by information obtained from other old members of the same tribe.

When the curare had been prepared, it was tried by the "poison-maker," for which purpose he slightly wounded a fowl. The fowl died after approximately fourteen minutes. Tests by the first author indicated that curare, as prepared by the Tecunas, is potent and contains the active paralyzing principle. Tests on frogs were also carried out by the first author with an extract of crude material of each component of curare, and



it has been ascertained that the bark of *Strychnos Castelnaii* contains the paralyzing principle. Certain species of *Strychnos* other than *S. Castelnaii*, as well as certain menispermaceous plants, were also found toxic. Whether these contain the active paralyzing principle or not remains to be seen, as experiments carried on in Brazil were not conclusive.

*Storing of crude material.* When bundles with crude material were brought from the forest, they were placed in the shade of trees and left there until the following morning. Indians claim that the crude material must be fresh, as otherwise the curare will not be effective. It is quite possible, however, that this is either superstition, or that by their crude methods they are unable to extract a sufficient quantity of the active principle from dried material to make their product effective.

*Preparation of material for extraction.* Early on the following morning, Indians began to prepare the crude material of *Strychnos Castelnaii* and of menispermaceous plants for extraction. Bundles with other curare ingredients were left intact. Material of *Strychnos toxifera*, *S. sp.* (Krukoff 7549, etc.), and possibly of some other species of *Strychnos* are occasionally also used. It is worthy of note, however, that these are not essential ingredients of curare of the Tecunas, and the poison is often prepared without them. Certain menispermaceous plants known to Indians as "atinupa" and "iku" are considered by them to be important components of curare. The name "atinupa" is applied by them to *Chondodendron polyanthum* and possibly to some other related species. The name "iku" refers to *Anomospermum reticulatum*. Preliminary tests showed that material of the latter was considerably less toxic than that of the former.

Stems of *Strychnos Castelnaii* were taken one by one and the outer bark was peeled off. The Indians do not use the inner bark and wood, claiming that they have no "poison." The bark was scraped off over leaves of the banana (*Musa* sp.) or of *Heliconia* sp. carefully spread out on the earthen floor of a hut. Care was taken not to lose any particles of valuable material. When they had a sufficient amount of shavings, these were carefully packed into a bundle made out of palm leaves. The bundle was well tied with vines in the middle and at both ends. The bundle with shavings was then placed in the coolest available place in the house and left there until the next day.

*Extraction.* Early on the following morning Indians began the extraction. Four sticks were driven in the earthen floor in the form of a square and about one foot apart. An empty clay container (A) was placed in this square. One end of the bundle was opened and protruding palm leaves were then secured to sticks, so that the bundle was suspended over the empty container (A), the upper end of the bundle being opened, the lower

end being tied. Cold clean water was slowly poured over the shavings. The water slowly dripped through the shavings and the extract was collected into the container (A) placed beneath the suspended bundle.

While the first extraction of the active principle was carried on, a fire was built and a large empty clay container (B) was placed over the fire. The extract was then carefully transferred from the container (A) to the container (B) and the operation was repeated, that is, clean cold water was again poured on the shavings, the extract was collected in the container (A) and then transferred to the container (B) for boiling. The container (B) was never removed from the fire.

It took from 20 to 30 minutes to complete a single extraction and about 2 litres of cold water was used each time. A rather strong fire was kept and it was raised each time when a fresh extract was added to the container (B). While the extract was boiling it was covered with a dirty white scum. The extract was carefully stirred with a calabash once every fifteen minutes.

While the extraction was carried on for the fourth, fifth and sixth times, the liquid was passed through the shavings twice and was well stirred with a stick before being transferred from the container (A) to the container (B) for boiling. While the extraction was carried on for the seventh and eighth time, the shavings were well squeezed out by hand. The seventh and eighth extractions lasted over one hour each. When the eighth extraction was completed the suspended bundle with shavings was removed, its open end was tied with a vine and the bundle was put aside.

The boiling of the extract was carried on for at least 8 hours. By this time it had boiled down to about a quarter of its original content. The extract, which before boiling had been of a light brownish color, assumed by this time the color of a strong decoction of coffee. The fire then was extinguished and the "poison" preparation was suspended until the next day.

*Preparation of curare.* On the following morning curare preparation was resumed. A small clay container (C) and a bag-like strainer, made out of a palm-blossom envelope (spathe) were brought. The extract was carefully strained by passing it three times through the strainer and then was placed in the container (C) on the fire for further boiling. From now on the fire was kept low, to insure only a gentle boiling.

While the extract was boiling, the container (A) which had been used for collection of the cold water extract from shavings and the strainer were carefully washed, the strainer was squeezed and washed by hand and this liquid was carefully collected and kept in the container (A), later to be used for the extraction of ingredients from other plants which are used in preparation of curare.

A bundle with roots of *Piper* sp. (*Krukoff* 7545) was brought. The roots were smashed and ground, the macerated mass was transferred into the container (B), some liquid from the container (A) was poured on, the entire mass then was poured into the strainer (straining was done three times), well squeezed by hand and finally placed in the container (C), which was still over the fire.

Fleshy tubers of *Aristolochia* aff. *arcuata* and of an undetermined cucurbitaceous plant were smashed and ground together with roots of *Petiveria alliacea* or an allied species. To this were added the macerated roots of *Piper* sp. (*Krukoff* 7545), and the remaining liquid from the container (A) was poured over the entire mass, which was then placed in the strainer and well squeezed by hand. Finally this filtered liquid (extract) was placed in the container (C) for boiling. An extract of the succulent portion of the stem and leaves of *Dieffenbachia seguina* var. *viridis* is also often used in the preparation of curare.

When the extract became of a somewhat syrupy consistency the fire was reduced. From now on the extract was continually stirred with a stick and was boiled down until the "syrup" became thick, gluey and of dark chocolate color. The container was then removed from the fire and left to cool until the next day.

*Method of strengthening curare.* On the following morning the curare was ready for use. Its potency was tried on some animal or bird, and if it was still weak, as on the present occasion, the following procedure was used to "make it more potent."

Roots of *Piper* spp. (*Krukoff* 7546 and 7635, which were used indiscriminately) were smashed and mixed together with shavings of the bark of roots of *Annona Ambotay*. A cold water extract of these was made, filtered through a strainer, and added to the curare, which was again placed on the fire and recomposed.

*Keeping of curare.* The poison afterwards is poured into small half-globular vessels made of clay, where it then becomes somewhat hard. The pots are tightly closed with small pieces of animal skin and well tied with a string. Curare is kept in the driest place in the house, as Indians claim that the atmospheric moisture deprives the poison of its strength. No information is available as to how the Tecuna Indians restore the strength of curare if it becomes weak during storage. They also claim that they do not know any antidotes for curare.

*Approximate quantities of various ingredients used in the preparation of curare by the Tecuna Indians.*

Shavings from the outer bark of *Strychnos Castelnaei*. . . . . 2 pounds

Shavings from the bark of <i>Chondodendron</i> aff. <i>polyanthum</i> and of <i>Anomospermum reticulatum</i> .....	8 ounces
Roots of <i>Piper</i> sp. ( <i>Krukoff</i> 7545).....	2.5 ounces
Roots of <i>Piper</i> sp. ( <i>Krukoff</i> 7546).....	1.5 ounces
Tuber of <i>Aristolochia</i> aff. <i>arcuata</i> .....	one tuber
Tuber of a cucurbitaceous plant ( <i>Krukoff</i> 7544).....	one tuber
Bark of roots of <i>Annona Ambotay</i> .....	1.5 ounces
Roots of <i>Petiveria alliacea</i> or of an allied species.....	1.5 ounces

*Specimens examined from the territory inhabited by the Tecuna Indians.*

#### ARACEAE

DIEFFENBACHIA SEGUINA (L.) Schott, var. VIRIDIS Engl.—*Krukoff* 7637, 7674.

#### PIPERACEAE

Three species of *Piper* enter into the preparation of curare as here described. One of these can be accurately matched with other herbarium material, but for the present we find it impossible to assign specific names to our specimens. *Krukoff's* field numbers are here cited in the hope that eventually the taxonomic uncertainty which envelops this difficult genus will be clarified.

PIPER sp.—*Krukoff* 7545, 7634. These specimens belong to the group of *P. obliquum* R. & P.

PIPER sp.—*Krukoff* 7546. Not matched by us in the herbarium of the New York Botanical Garden.

PIPER sp.—*Krukoff* 7635. Probably conspecific with *P. scalariforme* Trelease.

#### ARISTOLOCHIACEAE

ARISTOLOCHIA aff. ARCUATA Mast.—*Krukoff* 7542, 7633.

#### PHYTOLACCACEAE

PETIVERIA ALLIACEA L.—*Krukoff* 7638. Two other specimens (*Krukoff* 7543, 7639) represent a presumably allied species which is sometimes used by the Tecunas in place of *Petiveria alliacea*. Our material is undeterminable.

#### ANNONACEAE

ANNONA AMBOTAY Aubl. sens. lat.—*Krukoff* 7547, 7636.

#### MENISPERMACEAE

CHONDODENDRON POLYANTHUM Diels—*Krukoff* 7577, 7578.

CHONDODENDRON aff. POLYANTHUM Diels.—*Krukoff* 7535, 7579. These specimens differ from *C. polyanthum* by the obtuse or rounded rather than acute leaf apices and by the whitish rather than grayish tomentum.

ANOMOSPERMUM RETICULATUM (Mart.) Eichl.—*Krukoff* 7536, 7559–7564 inclusive, 7569.

#### LOGANIACEAE

STRYCHNOS CASTELNAEI Wedd.—*Krukoff* 7533, 7534, 7537, 7538, 7540, 7541, 7548, 7583–7625 inclusive, 7673, 7781, 7782, 7783. This extensive series of 54 herbarium numbers is further augmented by six collections from the Java territory. It is not to be assumed, because of this large number, that *S. Castelnaii* is a common plant. On the contrary, it is rarely met with in the forest, and *Krukoff*'s collections were made possible only by the aid of several crews of Indian helpers.

STRYCHNOS TOXIFERA Rob. Schomb. ex Benth.—*Krukoff* 7539.

STRYCHNOS sp.—*Krukoff* 7549, 7581, 7628–7632 inclusive.

#### CUCURBITACEAE

*Krukoff* 7544, in sterile condition, cannot accurately be referred to a genus. It may be a species of *Cyclanthera* or *Melothria*.

#### CURARE OF THE JAVAS

Java Indians now occupy the territory drained by some of the tributaries of the Rio Javary, and live on both Brazilian and Peruvian territory. They still extensively use blow-guns and curare. Below is described the preparation of the poison by Javas.

The Indians peeled off the bark of stems of *Strychnos* spp. while in the forest. Shavings were placed in a bundle made out of palm leaves. It is estimated that approximately three pounds of shavings were used on this particular occasion.

On the following morning the Indians commenced the preparation of the poison. Two large sticks were driven into the earth and two smaller ones were secured to these in a horizontal position. The bundle with shavings was tied to the sticks and the upper portion of the bundle was cut off, thus permitting water to be poured directly on the shavings. An empty container (A), made out of the bark of a tree, was placed beneath the bundle. Clear cold water was slowly poured on the shavings, the water dripped through the shavings, and the extract was collected in the container (A). It took approximately two hours to complete the first extraction. In the meantime a fire was built and a large clay container (B) was

placed over it. The extract from the container (A) was transferred to the container (B) for boiling. The fire was kept rather high. When the extract had boiled down to approximately four-fifths of its original content, a new extract (second extraction) was carefully transferred from the container (A) to the container (B). Four subsequent extractions were completed in the next four hours. The extract was transferred into the container (B) every time when its content had boiled down to approximately four-fifths of its original content. When the sixth extraction was completed the Indians allowed the extract to boil down to approximately one-fifth of its original content, and then removed the container (B) from the fire.

Early on the following morning the preparation of the poison was resumed and the container (B) was again placed on the fire. Bundles with crude materials of plants other than *Strychnos* spp. were brought in. Roots of two species of *Piper* were smashed and ground, the macerated mass was carefully washed in a container (C), strained, and the filtered extract was poured into the container (B).

The bark and some of the sapwood of the stems of *Capparis sola* (which is considered a very important component of curare by the Javas), *Roupala* aff. *adiantifolia*, *Duguetia* (probably) *Spixiana*, *Duguetia* aff. *asterotricha*, *Protium* sp., *Clavija* aff. *Poeppigii*, and an unidentified myrsinaceous plant were scraped off, the stems of *Ipomoea* sp. were obtained, the succulent portion of the stem and leaves of *Dieffenbachia* sp. were smashed, a few fruits of a red pepper (*Capsicum* sp.) were squeezed, and the entire mass was placed in the container (C), washed with cold water, well squeezed by hand, and filtered. The extract thus obtained was poured into the container (B) for boiling.

The Indians allowed the extract to boil down to one-third of its original content, then removed the container from the fire, transferred the extract to a smaller clay container (D) and left it to cool off. On the next morning the poison was ready for use. It was tried by the Indians on a small bird and found to be potent.

Javas seldom use *Strychnos Jobertiana* and *Strychnos* sp. (Krukoff 7654, etc.) considering that they furnish very inferior material. Tests on frogs were carried out by the first author with an extract of the bark of these two species and of *Strychnos Castelnaii*. It was ascertained that the bark of *Strychnos Castelnaii* contains the active paralyzing principle, while material of *Strychnos Jobertiana* and of *Strychnos* sp. was found considerably less toxic. Whether or not they contain the paralyzing principle remains to be seen, as experiments carried on in Brazil were not conclusive.

*Specimens examined from the territory inhabited by the Java Indians.*

#### ARACEAE

DIEFFENBACHIA sp.?—*Krukoff* 7672. This sterile specimen cannot with certainty be referred to *Dieffenbachia*, but in foliage it appears very close to *D. parviflora* Engl., which, however, has shorter petioles.

#### PIPERACEAE

PIPER sp.—*Krukoff* 7660. This specimen cannot be distinguished from the type of *P. cinereonervosum* Trelease.

PIPER sp.—*Krukoff* 7661. This appears nearly identical with the type of *P. tumidicondyli* Trelease.

#### PROTEACEAE

ROUPALA aff. ADIANTIFOLIA Kl.—*Krukoff* 7662. Our specimens have pinnate leaves up to 50 cm. long, with 8 or 9 pairs of strongly inaequalateral serrate leaflets. In foliage characters the plant appears closely related to *R. adiantifolia*, but the Amazonian species of the genus are too poorly known to permit accurate placing of sterile material.

#### ANNONACEAE

DUGUETIA sp., probably SPIXIANA Mart.—*Krukoff* 7659. This sterile specimen cannot be definitely determined.

DUGUETIA aff. ASTEROTRICA (Diels) R. E. Fries—*Krukoff* 7664. The material is also sterile.

#### CAPPARIDACEAE

CAPPARIS SOLA Macbride (*C. acutifolia* Macbride, not *C. acutifolia* Sweet)—*Krukoff* 7658, 7667. Our specimens exactly match *Klug* 961, the specimen which Macbride<sup>1</sup> has cited as the type of both *C. sola* and *C. acutifolia*.

#### BURSERACEAE

PROTIUM sp.—*Krukoff* 7666.

#### THEOPHRASTACEAE

CLAVIJA aff. POEPPIGII Mez—*Krukoff* 7665. Our specimen agrees well in foliage with *C. Poeppigii*, which is fairly common in Amazonian Peru. As the related species *C. tarapotana* Mez and *C. Hookeri* A. DC. are distinct primarily on the basis of floral characters, we cannot refer our sterile material with certainty.

<sup>1</sup> *Candollea* 5: 358, 359. 1934.

## MYRSINACEAE

*Krukoff* 7663. Probably a species of *Weigeltia* or *Stylogyne*.

## LOGANIACEAE

STRYCHNOS CASTELNAEI Wedd.—*Krukoff* 7648–7653 inclusive.

STRYCHNOS sp.—*Krukoff* 7654, 7655, 7656, 7675. These specimens are sterile and for the present cannot be referred to a species.

STRYCHNOS JOBERTIANA Baill.—*Krukoff* 7657.

## CONVOLVULACEAE

IPOMOEA sp.—*Krukoff* 7670, 7671. In foliage our sterile material resembles some specimens of *I. tiliacea* (Willd.) Choisy.

## SOLANACEAE

CAPSICUM sp.—No specimens available.

*A comparison of the botanical components of curare as prepared by the Tecunas and the Javas reveals the fact that Strychnos Castelnaii is the only species used by the members of both tribes. Three species of Piper used by the Tecunas are replaced by two other species of the same genus by the Javas. Dieffenbachia seguina var. viridis, used by the Tecunas, is replaced by another araceous plant by the Javas. Annona Ambotay, used by the Tecunas, is replaced by two species of Duguetia by the Javas. It is noteworthy that no species of Menispermaceae are used by the Javas, whereas Chondodendron polyanthum and Anomospermum reticulatum are important components of the curare of the Tecunas.*



## INDEX TO AMERICAN BOTANICAL LITERATURE 1933-1937

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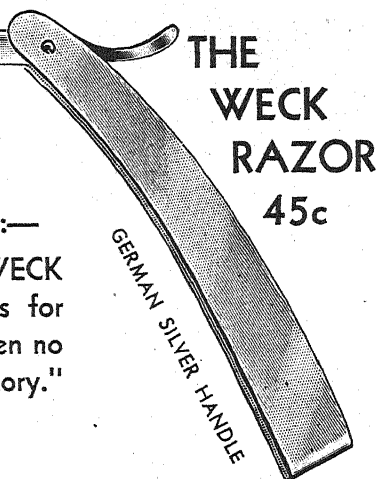


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23-10

## Histogenesis in the bamboo with special reference to the epidermis

WILLARD M. PORTERFIELD JR.

(WITH 22 FIGURES)

The first reference to the formation of the stomata in bamboo was made by Treviranus in 1820. In his extensive studies of the epidermis of plants he had occasion to examine the epidermis of *Bambusa arundinacea* and the first figure recording these observations appears in the *Vermischte Schriften* IV, T. I—fig. 24. The drawing while it incorrectly delineates the structure of the stoma interestingly enough constitutes the first record of the characteristic epidermal cells common to grasses generally and to bamboos in particular. Longitudinally parallel lines of cells are made up of two short cells successively alternating with long ones, and where occasionally the short cells are lacking a stoma takes their place. It is my purpose in this paper to trace the cell changes involved in the development of the epidermis from the end of the dermatogen through the stages of protodermal differentiation up to the period of cell specialization.

Considerable doubt existed among early investigators as to the origin of the subsidiary, or secondary, guard cells of the stomata. Hedwig (1784) in his figure showing a surface view of the epidermis of *Avena fatua* was the first to picture the stomata of grasses and he showed them with subsidiary guard cells. Duval-Jouve (1872) from his study of *Galilea mucronata* was quite certain that these cells together with the two smaller guard cells bordering the stomatal pore originated from a primordial mother cell by two successive divisions. This was in direct opposition to the conclusions of Strasburger (1866) who after a very thorough study of the development of stomata specifically stated that the subsidiary guard cells were produced by division of the epidermal cells that lie on either side of the mother cell and that the mother cell later undergoes one division to produce the two primary guard cells. The reasons Duval-Jouve gave for his opinion were: (1) the subsidiary cells appear to crowd the contiguous elements out of alignment; (2) they do not correspond in position with the cells of the contiguous line but alternate with them; (3) they correspond exactly with the primary guard cells; and (4) treatment with caustic potash separates the stomata as a whole from the contiguous cells the four cells remaining together. Pfitzer (1870) and De Bary (1884) corroborate Strasburger's careful observations and add further details from their own findings concerning the form and origin of the epidermis of grasses. Pfitzer held that the stomatal split between the adjoining guard

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cell walls is brought about as though by the pressing in of a wedge from above and below simultaneously. This theory brought him into contention with Reinhardt (1879) who formulated a theory known as the "internal pressure theory" by which the formation of the pore takes place as a result of great tension developed in the growing mesophyll through the accumulation of gases and water vapor in the air spaces with the result that the adjoining walls of the guard cells are forced apart. Among his significant contributions De Bary placed the origin of the stomata at the stage immediately following the time when dermatogen passes over into protoderm. With regard also to the epidermis he noted the intensive silicification of the upper of the two short cells. As yet, however, a histogenic delineation of these structures from the cytological viewpoint has not been undertaken. It is my intention to undertake this task and in so doing I propose to fill in the details of Strasburger's early picture with observations drawn from a study of bamboo meristems.

#### MATERIALS AND METHODS

This investigation was carried on at St. John's University, Shanghai, China. Fresh growing shoots of *Phyllostachys pubescens* H. de L. (*edulis* Carr.), *P. nigra* Munro, and *Arundinaria quadrangularis* Mak. were obtained as a source of the material required for study. Small blocks of growing meristem 3 mm. square were cut from the basal region of a young internode of the culm and similar square pieces were cut from the basal region of a young sheath leaf of each species. The material was then fixed in chrom-acetic of medium strength, embedded in hard paraffin (52°) and cut into sections 7 to 10 micra in thickness. Both tangential and transverse sections were cut. All permanent mounts were stained with Heidenhain's iron-haematoxylin.

We shall first consider the development of the stomata and then that of the epidermis proper.

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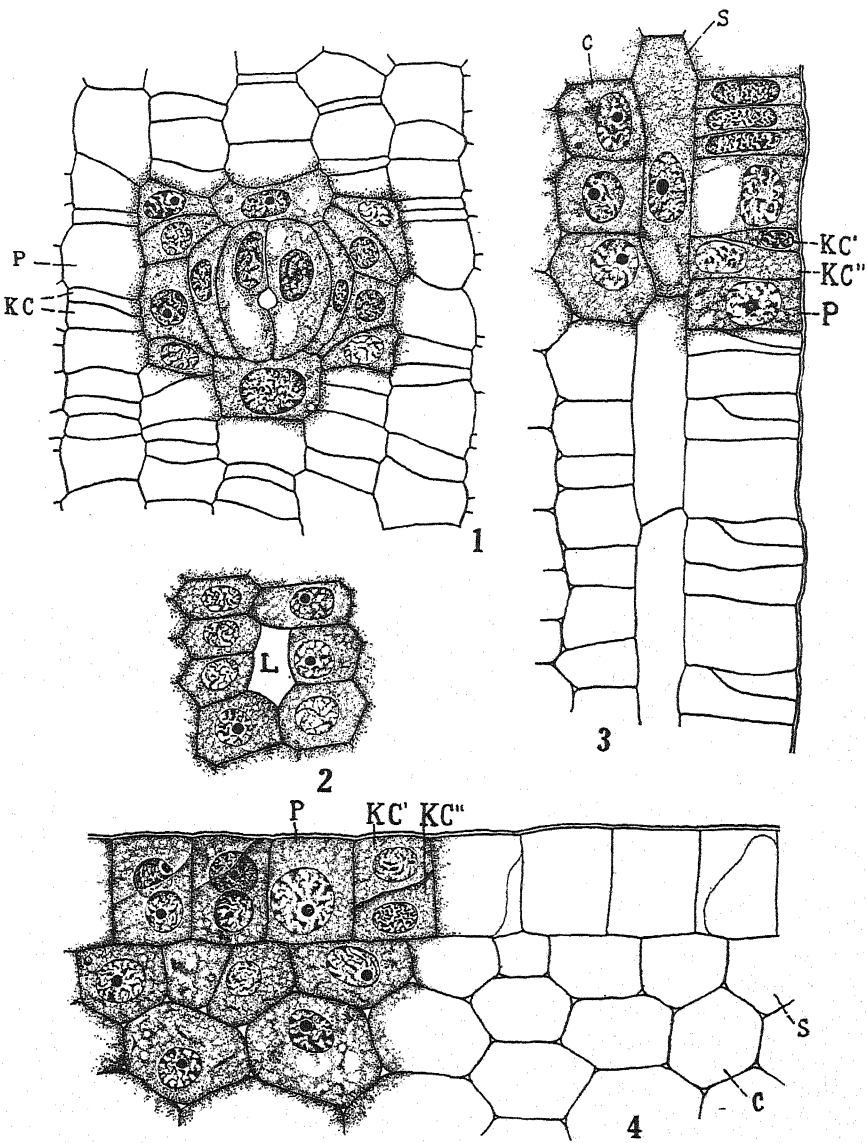
#### Explanation of plate 9

Fig. 1. Surface view of very early protoderm from the internode of a young shoot of *Phyllostachys pubescens* H. de L. A complete stoma is seen in the center flanked by primary and subsidiary guard cells together with the earliest "long" (P) and "short" (KC) elements of the protoderm.

Fig. 2. Air space in the subprotodermal layer underlying the stoma caused by separation of the cells.

Fig. 3. A radial longitudinal section showing three successive layers; the protoderm differentiating into long (P) and short (KC', KC'') elements of which the upper (KC') is wedge shaped; the subprotodermal layer of the cortex (S); and the cortical parenchyma (C) which is still meristematic.

Fig. 4. A transverse section showing the same elements as in figure 3 from above. All drawings were made with a camera lucida. The enlargement is 825 diameters.



PORTERFIELD: HISTOGENESIS IN BAMBOO

THE DEVELOPMENT OF THE STOMATA ON THE INTERNODES OF THE  
CULM AND SHEATH LEAVES OF BAMBOO

Tangential sections cut from a young internode of the bamboo culm while it is still enclosed by the sheath before it has elongated to any great extent will reveal protodermal elements in various stages of transition to becoming specialized epidermal cells and stomata. Comparatively short

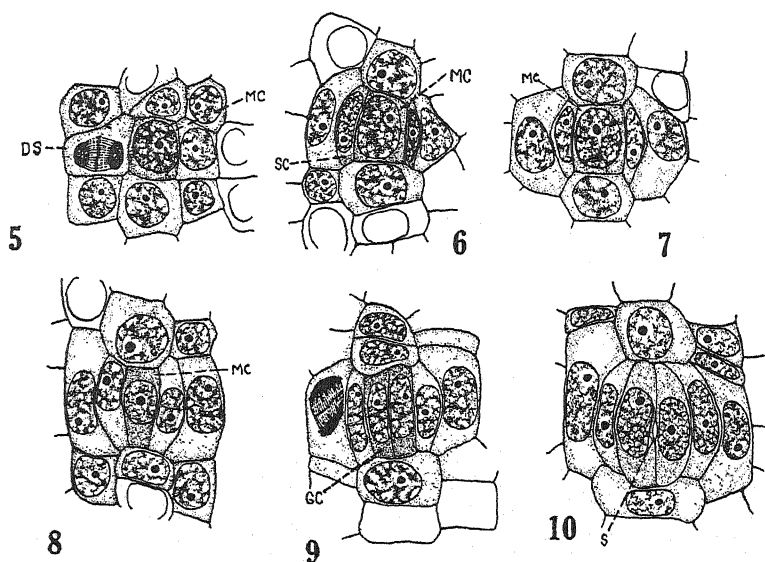


Fig. 5. Surface view of young protoderm from a tangential section of an internode from a shoot of *Arundinaria quadrangularis* Mak. Cell lateral to mother cell (MC) dividing to form subsidiary cells (DS).

Figs. 6 and 7. Mother cells (MC) flanked by subsidiary cells (SC).

Fig. 8. Same as 6 and 7 with elements elongated.

Fig. 9. Mother cell has divided to form primary guard cells (GC).

Fig. 10. Complete stoma showing pore (S). All figures  $\times 825$ .

cells, most of them broader than long, can be seen in vertical rows (plate 9, fig. 1). Mitotic figures are occasional. The nuclei are large and occupy about two-thirds of the cell cavity. The cytoplasm is dense and usually without vacuoles. Some of these cells become mother cells which will produce stomatal guard cells or the characteristic epidermal short cells. Such elements can be recognized by their large nuclei and slightly smaller diameters as Pfister (1870) pointed out in his study of the epidermis of *Zea Mays*. While the protodermal elements enlarge those destined to become mother cells retain their original size. The indentations in cell alignment

thus caused are filled by lateral extensions of the cells lying on either side of the mother cell. The lateral cells now prepare to undergo a segmental division. Their nuclei, if the cell happens to be elongated, move to a position opposite the extended arms bordering on the mother cell just as Strasburger (1866) showed in his figure 116, and pass through the stages of nuclear division (figs. 5, 11, 18, 22). The spindles form at right angles to the axis of cell alignment, but the cell plate instead of effecting an equational division of the cytoplasm cuts off an arching segment bordering on and concave to the mother cell (fig. 22). This method of division is found during development of the stomata on both the growing culm and the young sheath leaf. The mother cell is now flanked by two crescent shaped segments which become the subsidiary guard cells. The presence of the arching phragmaplast as seen in text figure 22 is undeniable proof of the origin of the subsidiary cells from the line of elements next the mother cell and not from the mother cell itself. The three cells together now appear as a barrel-shaped group lying within the limits of the cell line of which the mother cell is a part (fig. 7).

Cell stretching as well as cell multiplication is taking place while concurrently the mother cell undergoes a longitudinal equational division (figs. 19, 22). The stomatal group is now increased to four cells (fig. 9). In rapid succession the original lateral elements from which the segments were cut divide transversely (text fig. 9, plate 9, fig. 1), after which all visible signs of the original connection of the subsidiary guard cells with their lateral sources are lost. Sufficient evidence is not available to determine the exact mechanics involved in the formation of the stomatal pore but it is clearly evident that a limited region midway between the upper and lower ends in the juxtaposed membranes of the guard cells remains free to separate when the turgor of the guard cells reaches sufficient tension (plate 9, fig. 1, text fig. 10). In the subepidermal layer the creation of intercellular air spaces has occurred through failure of cell divisions to keep pace with mass growth. The cells as a consequence have drawn apart, and so free circulation of gases, especially of oxygen, is assured (plate 9, fig. 2). No chlorophyll is present at this time as the internode is enveloped by several layers of sheathing leaves which exclude the light.

The same general procedure for the formation of stomata is followed in the young sheathing leaves as in the internodes of the culm. The number of mother cells forming stomata, however, appear to be more numerous, in some cases so numerous as to alternate with every protodermal element in the line (figs. 19, 20, 22). Text figure 18 is noteworthy in that it records the fact that a lateral segment is frequently cut successively from one side and then the other of the same protodermal element when bordered on



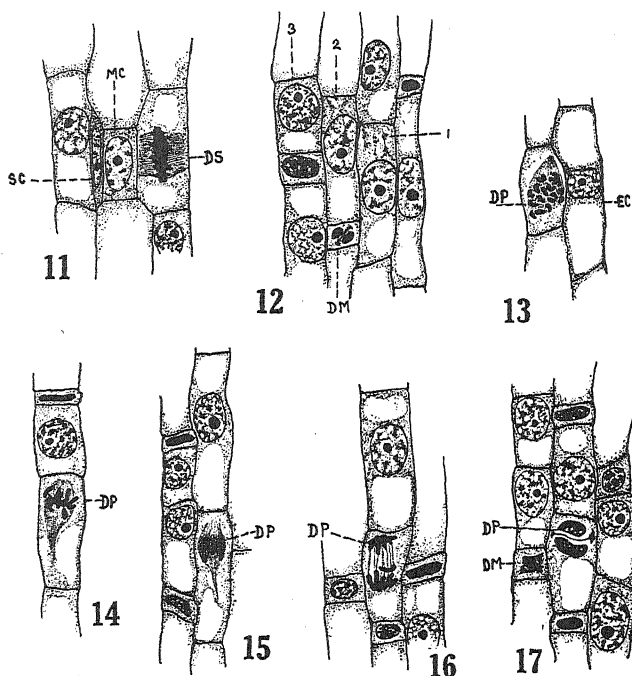


Fig. 11. Surface view of the protoderm from a tangential section of an internode from a shoot of *Phyllostachys nigra* Munro. One subsidiary cell (SC) is already formed flanking one side of the mother cell (MC) while division is taking place on the other side (DS) to produce the other.

Fig. 12. Protodermal cells with nuclei at different positions (1, 2, and 3) previous to division at the upper ends. DM, a dividing mother cell derived from the protoderm.

Fig. 13. Metaphase plate with 16 chromosomes in a dividing protodermal cell (DP). Typical "long cell" at the side (EC).

Figs. 14, 15, 16 and 17. Protodermal cells in various stages of division (DP) by which cells are being cut from the upper ends to form secondary mother cells. DM, secondary mother cell undergoing division.  $\times 825$ .

both sides by mother cells. The vacuolate nature of the cytoplasm in the cells shown in figures 11-20 is attributed to the fact that the material was taken from regions further advanced in development.

#### THE DEVELOPMENT OF THE EPIDERMIS IN THE CULM AND SHEATH LEAVES OF BAMBOO

The characteristic epidermis of grasses consists generally of parallel lines of alternate long and short cells interspersed with strips containing stomata instead of short cells. In leaves the former predominate. In the bamboo long rectangular cells alternate with two short cells as Treviranus

(1820) discovered. The uppermost of the two later becomes practically solid and acquires the appearance of an inverted cone of glass. This is due to the deposition of silica as described by De Bary (1884), which the bamboos contain in abundance.

The first step after the differentiation of the primary stomata as described above is the restriction of cell divisions to alternate elements of the protodermis (plate 9, fig. 3). The general effect is the lengthening of some cells and the shortening of others. With the gradual cessation of cell divisions cell stretching becomes more pronounced especially in the long cells. General elongation of the culm and the sheath takes place

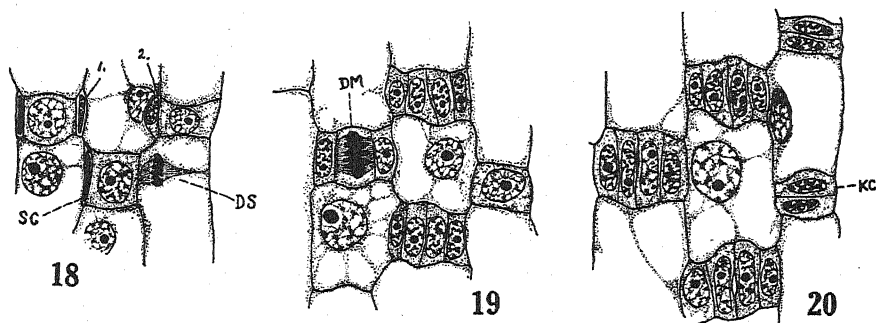


Fig. 18. Surface view of the protoderm of a sheath leaf of *Phyllostachys pubescens* H. de L. from a tangential section. Subsidiary cells (1 and 2) cut from opposite sides of the same protodermal cell. SC, subsidiary cell; DS, a dividing lateral cell with a horizontal spindle at its upper end.

Figs. 19, 20. Parallel lines of typical protodermal cells alternating with stomata. In some lines "short cells" (KC) take the place of stomata.  $\times 825$ .

basipetally internode by internode thereby establishing a histogenic gradient from the base upward in each internode successively. It is worth noting that at this period of growth mechanical support in the meristematic regions and protection from injury are taken care of by the stiff collar formed by the enveloping sheathing leaves. Internally turgor pressure plays an important part in the support of the young culm.

Continued examination shows that as the protodermal cells elongate the nuclei appear to remain in the upper half of the cell (figs. 12, 17, 22), or if they do locate in the central region, the cytoplasm remains dense in the part of the cell above the nucleus while below a vacuole makes its appearance implying regional differentiation (fig. 12). This introduces the question of whether there is a definite acropetal tendency in nuclei of actively elongating elements comparable to the behavior of the tube nucleus in an advancing pollen tube, or whether in such cells the nucleus is passive

and is carried forward through the push exerted by the backward extension of the cell.

The nucleus at the upper end of the cell in the most active period soon enters the prophase preparatory to undergoing division. Figures 14-17 show respectively metaphase, early anaphase, late anaphase and telophase of a dividing nucleus by which unequal cell division is accomplished and the small upper initial is cut off. This cell remains isodiametric and becomes a mother cell (fig. 21) which may either produce secondarily a stoma as described above or undergo a second transverse but unequal division (figs. 12 and 17) to form two short cells (plate 9, fig. 3 ( $KC'$ ,  $KC''$ )). These remain short but later differentiate, the upper becoming a siliceous sclereid, the lower an isodiametric element with thickened walls. It should be noted that the upper of the two short cells (plate 9, fig. 3 ( $KC'$ )) in a radial longitudinal section appears to be a wedge-segment of the lower which undoubtedly accounts for its conical shape later.

#### DISCUSSION OF CYTOLOGICAL FEATURES

The average meristematic elements in the bamboos are very small. Viewed from the surface they range in length from 5 micra or even less to 15, and in width from 13 to 20 micra. The nuclear divisions connected with the formation of the stomata and the special epidermal cells appear to proceed in the usual manner. The chromosomes, however, are very minute and have a tendency in some stages of mitosis to clump together, so that it is difficult to distinguish them (figs. 9, 11, 19, 22). Preliminary counts made at metaphase in *Phyllostachys nigra* show 16 chromosomes (fig. 13). The location of the nucleus, on the other hand, as it prepares to undergo the initial histogenic divisions seems to be out of the ordinary as previously noted and the achromatic figure displays unusual features. The position of the nucleus seems to have no connection with symmetry, balance, or space relations within the cell while the spindle and the subsequent phragmoplast are irregular in the same degree but in different ways. The polar position of the nucleus previous to the production of mother cells in the one instance and its position opposite the mother cell in the stages leading to the origin of the subsidiary guard cells in the other are determined probably by physiological rather than mechanical influences. The spindles in the two respective cases are necessarily determined by the positions of the nuclei in connection with which they develop, but their different orientation suggests that the direction of osmotic "flow" is a governing factor, the cell plate forming at right angles to the direction of greatest activity. The curving phragmoplast of the divisions which form the subsidiary guard cells (fig. 22) may be explained

on this basis by postulating great physiological activity in the nucleus and cytoplasm of the adjoining mother cell toward which the concave pole of the phragmoplast always faces.

In shape the spindles of both these divisions bear a relation to the amount of space around each and to the way that space is apportioned. Text figures 14 and 15 show spindles in which the upper poles where the space is confined are rounded, while at the lower poles where the cell extends far beyond the spindle becomes attenuate in outline. Conversely, in the segmental division by which the subsidiary guard cells originate (figs. 11, 22) and in the longitudinal division of the mother cell (text fig. 19) the configuration of the spindles is restricted, the poles being much flattened by reason of the limited space available.

In addition to the position of the nuclei at division and the differences in spindle configuration there is the concurrent problem of cytokinesis. In the two special histogenic divisions described nuclear divisions were assumed to have been regular and equal, but it is quite obvious that the partition of the cytoplasm was un-

equal. This unbalanced allotment of cytoplasm to the daughter cells renders the ratio of chromatin to cytoplasm in the two daughter units quite different in both cases. Is this difference in the nucleoplasmic ratio significant in the diverging line of development taken by the two daughter cells? It seems to assure in the case of the smaller daughter cell the restoration of the nucleoplasmic ratio characteristic of an early meristematic cell so that it may function if necessary as a mother cell, and in the case of the larger daughter cell continued progress in histogenesis. To what extent cytoplasmic factors are significant in histogenic development can not at present be told but it is certain that they can not be ignored. And if the cytoplasm can not be ignored neither can the nuclear factors of which not the least important are the hereditary genes. If certain protodermal cells become constituted as histogens, does their divergent descent imply a divided heredity, and if that is so, can the nuclear divisions which pro-

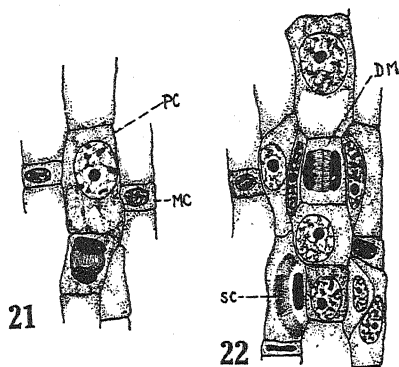


FIG. 21. Surface view of the protoderm of a sheath leaf of *Phyllostachys nigra* Munro from a tangential section. Typical protodermal cell (DC) preparing to divide at its upper end. MC, secondary mother cell derived from protoderm.

FIG. 22. An original mother cell (DM) dividing longitudinally. SC, a dividing lateral cell with arched phragmoplast cutting out a subsidiary guard cell  $\times 825$ .

duce a histogen be properly called mitotic? An assumption of segregating genes rather than the distribution of identical gene duplicates in this case and from this point of view is justified. A gradual breakdown of hereditary gene aggregates accompanied by periodic distributions of gene units during morphogenesis in all its different phases calls to mind the behavior of Weismann's biophors and the disintegrating ids, and parallels in general his conception of the mechanics of heredity in relation to morphogenesis.

#### CONCLUSIONS

In conclusion it can definitely be stated in regard to the origin of the stomata in bamboo that the evidence here presented supports the statements made by Strasburger (1866) for grasses, that the subsidiary guard cells are derived by cell division from the adjacent elements of the epidermis and not from the mother cell, that in this process the position of the nucleus is significant, and that the formation of the subsidiary guard cells takes place before and not after the mother cell divides to form the primary guard cells with the stoma between. In addition I have established the fact that unequal cytokinesis following nuclear division is accomplished by the arching movement of the phragmoplast comparable to that made by the vegetative nucleus in a pollen grain of *Lilium* when it divides to produce generative cell and tube nucleus. In regard to the origin of the true epidermis of bamboo my studies have shown that the three types of epidermal cells arise from protodermal cells in common with the stomata and that by unequal cell division in which again the position of the nucleus is significant a small cell is cut from the upper end of an elongating one. This cell finally produces also by unequal transverse division two more cells, the upper one wedge shaped, the lower one isodiametric, to round out the epidermal complement, or it may secondarily produce a stoma as previously described.

In regard to the time of origin my findings support De Bary's statement (1884) that the stomata do not originate all at one time but successively as growth proceeds. I find that from the standpoint of origin the stomata of bamboo fall naturally into two classes: (1) those which develop from primary meristematic tissue (figs. 1 and 5-10); and (2) those which originate from mother cells secondarily produced in the advanced protoderm. The production of the epidermis proper is not as clear because of the generalized character of the elements, but it seems to commence later involving at first original protodermal cells (plate 9, fig. 3) and later mother cells (figs. 12 and 17).

In the final analysis the development of the specific complements that make up the epidermis of bamboo can be referred to those same elemental

processes which operate in general to form the plant body. Histogenesis like morphogenesis "aside from differentiation, in the metaphytes is a matter of specifically oriented cell enlargement (plate 9, fig. 3) and specifically oriented cell divisions (compare figs. 11 (*DS*), 18 (*DS*), 22 (*SC*)) however they may be determined" (Harper, 1929).

#### SUMMARY

1. Material inclusive of culms and sheath leaves from shoots of *Phyllostachys pubescens* H. de L., *P. nigra* Munro, and *Arundinaria quadrangularis* Mak. was studied with reference to the origin of stomata and epidermis.

2. The development of stomata and epidermis in culms and sheath leaves was found to be similar except that in the case of sheaths the stomata were more numerous.

3. The early protoderm is composed of small cells mostly broader than long ranging from 5 to 15 micra in length and from 13 to 20 micra in width having large nuclei which occupy two-thirds of the cell cavity and lie in dense cytoplasm.

4. The subsidiary guard cells of the stoma are produced by divisions cutting off lenticular segments of the protodermal cells lying next the mother cell.

5. The mother cell divides longitudinally after the appearance of the subsidiary guard cells to form primary guard cells which flank the stoma proper.

6. The production of the epidermal complement of one long with two short cells above begins with a primary division by which a small isodiametric element is cut from the upper end of a long cell and is constituted a mother cell.

7. A further division of the small mother cell takes place—somewhat unequally and obliquely—to form the two "short" cells, the uppermost of which according to its shape eventually becomes obconical.

8. The same mother cell may also produce a stoma.

9. Stomata are first developed when the dermatogen passes over into protoderm, then secondarily as growth proceeds from mother cells differentiated by the protoderm.

10. The epidermal cells in point of time develop later than the stomata and from protoderm and protodermal derivatives.

11. A cytological study disclosed certain outstanding features in the cell divisions involved in the histogenesis of the epidermis: (1) the ex-centric position of the nucleus preliminary to the formation of subsidiary guard cells and to the production of mother cells by the protoderm; (2)

variations in spindle configuration and behavior exemplified in the divisions resulting from (1).

12. A preliminary count of the chromosomes of *Phyllostachys nigra* Munro gave  $16 = 2n$ .

I wish to express my appreciation of Dr. A. B. Stout's cooperation in making it possible for me to avail myself of Miss Bessie Vasdof's valuable assistance in the translating work necessary to the preparation of this paper.

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## Experiments on latent infection of resistant varieties by the loose and covered smut of oats<sup>1,2</sup>

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The host-parasite relationship of the loose and covered smuts with the various varieties of cultivated oats permits a systemic infection as opposed to the local infection of such smuts as *Ustilago Zeae* (Beckm.) Ung. on corn. Thus the loose smut, *Ustilago Avenae* (Pers.) Jens. and the covered smut *Ustilago levis* (Kell. and Sw.) Magn. of oats are associated with the host throughout the lifetime of the latter, infection taking place in the very young embryo or seedling and sporulation occurring at maturity. Before the sporulation of the parasite it appears that both normal and smutted plants show similar characteristics. It is difficult to distinguish between a smutted and non-smutted plant much before the heading-out period. At maturity, in the smutted plant, the spores partly or entirely take the place of the grain. Recently, it has been thought that even if the mycelium does not evidence itself in sporulation, such invisible or "latent infection" is detrimental to the plant as shown in lowered yield, height, and vigor. More recently, this has been extended to include plants resistant to various physiologic races of oat smuts. It is thought that such plants, inoculated with smuts to which they are normally resistant, show the effect of such inoculation with a lessened yield, smaller size, lower culm production as compared with the non-inoculated controls.

### REVIEW OF LITERATURE

Recently, Hubbard and Stanton (1934) undertook to show that covered smut of oats, *Ustilago levis* (Kell. and Sw.) Magn. adversely affected resistant varieties, even if no smut became visible in the growing plants. They concluded that "the yield per row, the number of plants, panicles and culms per row, and the height of the plants of resistant as well as susceptible varieties were reduced by smut infection." Earlier experiments by Stanton *et al* (1930) were taken to indicate that the smut mycelium might be present in the culms of resistant plants without sporulating. They also thought that such latent infection might unfavorably affect the yield of grain per plant, the number of plants, culms and panicles per row and the height of plants. Bayles and Coffman (1929) working with Markton, furnished data which showed a reduction in seedling emergence and plant maturation from inoculated as compared with non-

<sup>1</sup> Accepted in partial fulfillment of the requirements for the degree of Master of Science at Washington Square College, New York University.

<sup>2</sup> Brooklyn Botanic Garden Contribution No. 78.



inoculated seed. More recently, Stevens (1936) studied the effect of latent infection on the smut-resistant Markton oat. He concluded that "the smut-resistant Markton oat variety is injured by inoculation and infection with smut that results in the killing of many seeds and thus reduces the stands." It is significant to note his assertion that "after the plants emerge and become established, however, there appear to be no detrimental effects." Welsh (1932) in his study of the effect of the smut fungus on the development of rust states that the "smut infection in oat plants, although not evident in the panicles, may bring about a marked reduction in vigor." He could, however, find no difference in the amount of rust infection between smut inoculated and uninoculated seedlings under greenhouse conditions, while under field conditions, mature plants inoculated but free from smut were rusted more heavily than uninoculated plants. Hart (1931) found, in Anthony oats, inoculated with spores of the covered and loose smuts of oats, no indication that rust resistance was altered by smut infection. Zade (1932) contributes the information that a non-sporulating infection of loose smut, *Ustilago Avenae*, caused reduction in the length of culms and panicles and resistance to winter injury. Kolk (1930) however, observed that the smut mycelium in inoculated seed of Black Mesdag does not penetrate further than the coleoptile and that the mycelium there is not plentiful. In the non-resistant variety she studied, the observation was made that the mycelium rapidly reaches the growing point. Woolman (1930) reports the same phenomenon in his study of the cytology of smut infection in the wheat plant.

In their attack on the problem of latent infection, Hubbard and Stanton (1934) studied Black Mesdag, Markton and Navarro as the resistant varieties with Victory as the non-resistant control. Their experiments were conducted entirely under limited field conditions, with a high plant mortality. No cytological examinations were made. There is also the indication that a new physiologic race of *Ustilago levis* recently described by Reed (1932) which moderately affects Black Mesdag, was present either in the field or in the smut collection used for inoculation by these workers. Stevens (1936) studied Markton as the resistant variety with Idamine as the susceptible control. Here, too, the work was done entirely under limited field conditions. Again, no cytological examinations were made to ascertain the presence of the fungus within the plant tissue.

Considering these facts, it was thought worth while to conduct experiments to further test the validity of the hypothesis that resistant oat varieties, inoculated with smut, are adversely affected because of the presence of a non-sporulating infection.

Dr. G. M. Reed of the Brooklyn Botanic Gardens suggested the investigation here to be described. The writer is grateful to him for the materials furnished by him and for his constant advice and stimulation.

#### EXPERIMENTAL

The oat varieties, Black Mesdag, Markton, Early Champion, Monarch, Scottish Chief and Gothland of *Avena sativa*, the variety Fulghum of *A. byzantina* and strains of *A. strigosa* and *A. brevis* were used in these experiments. Markton is highly resistant to the physiologic races of oat smut. Black Mesdag, however, has recently been found by Reed (1932) to be susceptible to infection by a new physiologic race of *U. levis* (race L<sub>12</sub>) which also infects Fulghum. Monarch is highly susceptible to the Missouri race of covered smut (L<sub>1</sub>) while it is resistant to the loose smut (race A<sub>1</sub>). Gothland is highly susceptible to the Missouri race of the loose smut, *U. avenae* (race A<sub>1</sub>) while Scottish Chief is moderately susceptible to this smut. Both are highly resistant to the covered smut, *U. levis* (race L<sub>1</sub>). Early Champion is susceptible to both loose and covered smuts, (races A<sub>1</sub> and L<sub>1</sub>). *A. brevis* and *A. strigosa* are highly susceptible to the Wales collection of covered smut (race L<sub>2</sub>) in use here at the Brooklyn Botanic Garden. The inoculations were as follows:—With A<sub>1</sub> and L<sub>1</sub>, the varieties Markton, Black Mesdag, Monarch, Gothland, Scottish Chief and Early Champion. The strains of *A. strigosa* and *A. brevis* were inoculated with L<sub>2</sub>. Fulghum was inoculated with L<sub>12</sub> as were groups of Black Mesdag and Monasch. Groups of uninoculated plants of each variety were planted as controls.

Experiments were undertaken both in the greenhouse and in the field. All the oat varieties mentioned above were used in a first planting on September 24, 1935 in the greenhouse (Series A). Early Champion, *A. strigosa* and *A. brevis* were not included in a second planting on October 22, 1935 (Series B). The greenhouse plants were collected at various intervals and examined cytologically for the smut mycelium and for height and other characters. Those in the field were used mainly for the determination of height, yield, production of culms and heading and ripening. All plants were germinated in waxed paper cups from seed dehulled by hand. The sand in the cups had a constant moisture content of 20 per cent. The cups were kept at a temperature of 20 degrees C. in constant temperature baths. The seeds to be planted were examined under the dissecting microscope after dehulling, and all seeds found to be injured in any way were discarded. They were then blackened with smut spores in coin envelopes. Twenty seeds per cup were permitted to remain in the constant temperature tank for four days. The plants were then

removed from the tank and permitted to stand for two more days in the greenhouse at which time they were transplanted to pots in the greenhouse or to the field.

Twenty plants were space-planted in a good sandy loam at equal distances in 12 inch Azalea pots. At 5, 14, 21, 35 and 65 day intervals, two of the plants were removed for examination. Ten plants in each pot were permitted to grow to maturity so that a count of smutted plants might be made. Examination of the growing point was made by fixing the plants in a formol-alcohol-acetic acid fixative of the following composition:—

Formalin, 40 per cent. ....	10 parts
Alcohol, 85 per cent. ....	85 parts
Acetic acid, glacial. ....	5 parts

The tissue was then dehydrated in the various alcohols, imbedded in paraffin and sectioned at 10–20 $\mu$ . Methyl blue in lacto-phenol was used for staining. By comparing with material fixed in various other fluids such as Flemming's weak and strong fixatives and chrom-acetic, this was found to be a convenient and very reliable procedure. In other cases, especially in the examination of the coleoptile and other tissues, the fresh tissue was sectioned by hand and mounted immediately in lacto-phenol and methyl blue. This was allowed to stand for from 1–2 hours, then washed several times with the lacto-phenol medium and examined. Such mounts remained satisfactory for examination for a period of two to three months.

In the field, twenty-five plants per row were space-planted on April 8, 1936 in a well mixed good, loam soil three inches apart in 6 $\frac{1}{4}$  foot rows, 1 foot apart. Black Mesdag was inoculated with physiologic races of both loose and covered smut to which it is highly resistant. Gothland was inoculated with a physiologic race of covered smut to which it is not susceptible. Monarch was inoculated with a race of loose smut to which it is highly resistant. *A. brevis*, however, was inoculated with a race of the covered smut, *Ustilago levis*, which generally infects it to the extent of 5 per cent. In Gothland, Monarch, and *A. brevis*, 12 rows of non-inoculated plants alternated with 12 rows of inoculated plants, so that a row of treated plants was adjacent to a row of untreated plants. In the case of Black Mesdag, 12 rows of non-inoculated seed were followed by 12 rows of seed inoculated with the loose smut. These rows, in turn, were followed by 12 rows of seed inoculated with the covered smut. The total planting consisted of 108 rows. A border row of Monarch seed was planted to prevent unequal growth of the end plants of each row. The 108 rows were in

three plots of 36 rows each. The non-inoculated seed was planted first to prevent contamination.

The height of the plant was taken from the first node to the lowest

TABLE 1  
*Incidence of mycelium in growing point, and coleoptile of greenhouse plants*

VARIETY	INOCULATED WITH	MYCELIUM IN GROWING POINT		MYCELIUM IN COLEOPTILE	
		No. Examined	% Infected	No. Examined	% Infected
Black Mesdag	Non-inoc.	18	0	14	0
Black Mesdag	<i>U. avenae</i> (1)	18	0	14	35.8
Black Mesdag	<i>U. levis</i> (1)	7	0	5	60.0
Black Mesdag	<i>U. levis</i> (12)	18	57	14	64.3
Scottish Chief	Non-inoc.	18	0	14	0
Scottish Chief	<i>U. avenae</i> (1)	18	47.7	14	57.1
Scottish Chief	<i>U. levis</i> (1)	18	0	14	28.6
Gothland	Non-inoc.	18	0	14	0
Gothland	<i>U. avenae</i> (1)	18	79	14	64.3
Gothland	<i>U. levis</i> (1)	18	0	14	64.3
Monarch	Non-inoc.	18	0	14	0
Monarch	<i>U. avenae</i> (1)	18	0	14	28.6
Monarch	<i>U. levis</i> (1)	18	93.5	14	85.7
Monarch	<i>U. levis</i> (2)	7	0	5	40.0
Monarch	<i>U. levis</i> (12)	18	85	14	92.8
Markton	Non-inoc.	18	0	14	0
Markton	<i>U. avenae</i> (1)	7	0	5	40.0
Markton	<i>U. levis</i> (1)	18	5	14	28.6
Early Champion	Non-inoc.	7	0	5	0
Early Champion	<i>U. avenae</i> (1)	7	83.3	5	80.0
Early Champion	<i>U. levis</i> (1)	7	59.1	5	100.0
<i>Avena brevis</i>	Non-inoc.	7	0	5	0
<i>Avena brevis</i>	<i>U. levis</i> (2)	7	59.1	5	80.0
<i>Avena strigosa</i>	Non-inoc.	7	0	5	0
<i>Avena strigosa</i>	<i>U. levis</i> (2)	7	100	5	100
Fulghum	Non-inoc.	18	0	14	0
Fulghum	<i>U. levis</i> (12)	18	47.1	14	64.3
Total		376		238	

NOTE: The specimens examined for growing point infection and coleoptile infection were different plants.

rachis of the tallest panicle. Where the immature plants were measured in the greenhouse, the height was taken from the soil line to the highest leaf node. The number of culms were taken as a count of all the fruiting culms. For the determination of yield of grain, the panicles were removed at the lowest rachis, placed in manila envelopes and weighed.

## EXPERIMENTAL DATA

A summary of the data on the greenhouse experiments is to be found in tables 1, 2, and 3.

TABLE 2

*Height of greenhouse plants at various intervals*

VARIETY	INOCULATED WITH	HEIGHT OF PLANTS IN CM.			% SMUTTED AT MATURITY
		30 DAYS (40 PLANTS)	90 DAYS (20 PLANTS)	MATURITY (20 PLANTS)	
Black Mesdag	Non-inoc.	6.3	37.5	130.6	0
Black Mesdag	<i>U. avenae</i> (1)	5.9	32.8	128.0	0
Black Mesdag	<i>U. levis</i> (1)	a) 6.3	39.3	A 133.6	0
Black Mesdag	<i>U. levis</i> (12)	6.6	34.4	138.6	40
Scottish Chief	Non-inoc.	5.4	25.5	155.0	0
Scottish Chief	<i>U. avenae</i> (1)	5.6	32.1	141.9	60
Scottish Chief	<i>U. levis</i> (1)	b) 5.1	29.4	120.0	0
Gothland	Non-inoc.	5.7	29.1	162.4	0
Gothland	<i>U. avenae</i> (1)	5.8	27.8	107.1	100
Gothland	<i>U. levis</i>	5.7	28.3	167.7	0
Monarch	Non-inoc.	4.0	29.5	120.3	0
Monarch	<i>U. avenae</i> (1)	c) 3.9	1) 32.4	153.3	0
Monarch	<i>U. levis</i> (1)	4.6	24.7	124.2	100
Monarch	<i>U. levis</i> (2)	4.6	30.2	A 138.0	0
Monarch	<i>U. levis</i> (12)	4.1	27.4	121.6	90
Markton	Non-inoc.	d) 5.7	2) 20.7	128.5	0
Markton	<i>U. avenae</i> (1)	e) 5.8	24.4	A 129.5	0
Markton	<i>U. levis</i> (1)	5.9	21.8	121.6	0
Early Champion	Non-inoc.	4.9	30.9	A 136.6	0
Early Champion	<i>U. avenae</i> (1)	5.1	3) 28.7	A 130.9	70
Early Champion	<i>U. levis</i> (1)	4.8	29.2	A 122.2	70
<i>Avena brevis</i>	Non-inoc.	2.2	23.1	A 131.3	0
<i>Avena brevis</i>	<i>U. levis</i> (2)	2.1	20.1	A 131.4	90
<i>Avena strigosa</i>	Non-inoc.	2.5	13.1	A 90.2	0
<i>Avena strigosa</i>	<i>U. levis</i> (2)	2.3	10.3	A 67.6	90
Fulghum	Non-inoc.	3.8	14.0	88.6	0
Fulghum	<i>U. levis</i> (12)	3.8	15.4	97.2	80

Height was taken from the soil surface to the highest node.

*U. avenae* (1)—Physiologic form of the Missouri smut collection.

*U. levis* (1) —Physiologic form of the Missouri smut collection.

*U. levis* (2) Physiologic form of the Wales smut collection.

*U. levis* (12)—Physiologic form of the Fulghum smut collection.

a, b, c, d, e —1 plant lost during germination. The average is therefore taken of the 39 plants remaining.

1, 2, 3 —2 plants lost. The average of these 90 days old plants and those of the same series in the "maturity" column is taken therefore from the plants remaining. The 90 days old plants are the same as those measured at maturity.

A —Refers to plants not included in Series B, planted later.

## PRESENCE OF THE SMUT MYCELIUM

In only one case, i.e. Markton, in one plant inoculated with *U. levis* race L<sub>1</sub>, did examination of a resistant variety show the smut mycelium in the growing point or in any of the tissues of the plant excepting the

TABLE 3  
*Presence of the smut mycelium throughout plant body*

VARIETY	INOCULATED WITH	NO. OF PLANTS STUDIED	PRESENT IN NODES	PRESENT ONLY IN CROWN ROOT NODE*
Black Mesdag	Non-inoc.	10	0	0
Black Mesdag	<i>U. avenae</i> (1)	10	0	0
Black Mesdag	<i>U. levis</i> (1)	5	0	0
Black Mesdag	<i>U. levis</i> (12)	10	4	1
Scottish Chief	Non-inoc.	10	0	0
Scottish Chief	<i>U. avenae</i> (1)	10	6	1
Scottish Chief	<i>U. levis</i> (1)	10	0	0
Gothland	Non-inoc.	10	0	0
Gothland	<i>U. avenae</i> (1)	10	7	1
Gothland	<i>U. levis</i> (1)	10	0	0
Monarch	Non-inoc.	10	0	0
Monarch	<i>U. avenae</i> (1)	10	0	0
Monarch	<i>U. levis</i> (1)	10	9	1
Monarch	<i>U. levis</i> (12)	10	9	0
Monarch	<i>U. levis</i> (2)	5	0	0
Markton	Non-inoc.	10	0	0
Markton	<i>U. avenae</i> (1)	5	0	0
Markton	<i>U. levis</i> (1)	5	0	0
Early Champion	Non-inoc.	5	0	0
Early Champion	<i>U. avenae</i> (1)	5	4	1
Early Champion	<i>U. levis</i> (1)	5	2	2
<i>Avena brevis</i>	Non-inoc.	5	0	0
<i>Avena brevis</i>	<i>U. levis</i> (2)	5	4	0
<i>Avena strigosa</i>	Non-inoc.	5	0	0
<i>Avena strigosa</i>	<i>U. levis</i> (12)	5	4	1
Fulghum	Non-inoc.	10	0	0
Fulghum	<i>U. levis</i> (12)	10	7	1

Every second node sectioned by hand and examined in methyl blue in lacto-phenol.

\* Except in Monarch, inoculated with *U. levis* (1) the smut mycelium also appeared in the three nodes above the crown root node but never higher.

coleoptile. However, Smith and Bressman (1931) have shown that Markton may be susceptible to various races of the covered smut. Infection of the coleoptile in resistant plants was to the extent of 28.6 per cent to 64.3 per cent. It consisted of a few hyphae, while in the susceptible varieties the mycelium ramified through the coleoptile tissue as a richly branching network. In all cases in the resistant varieties, the smut mycelium had

disappeared from the coleoptile by the end of the thirtieth day. It did not, however, reach any other portions of the plant in the resistant varieties, while in the non-resistant it rapidly reached the growing point. In the non-resistant plants, the coleoptile infection varied from 57 per cent in some varieties to 100 per cent in Early Champion inoculated with the physiologic race  $L_1$  of *Ustilago levis*. Where mycelium was found in the growing point it was found in varying amounts in the culm of the plant. In only 9 cases out of 65 infected plants (table 3), when no evidence of the smut mycelium was to be found at the growing point, mycelium was found below the growing point. In those cases, the mycelium was present in the crown root node and in a few nodes immediately above it.

#### SURVIVING GREENHOUSE PLANTS

There was 100 per cent germination except in those series marked a, b, c, d, e, (table 2). In these one seed out of twenty failed to germinate. In addition, all plants left to mature, except those series marked 1, 2, 3 (table 2) showed 100 per cent maturation. In these series, two plants died. In Monarch, these plants were infected with a wet-rot (probably a *Fusarium*). No other plants showed this infection. Thus, there was practically 100 per cent germination and survival of both inoculated and non-inoculated resistant and non-resistant greenhouse plants.

#### HEIGHT OF PLANTS

In the greenhouse, the only measurement found convenient was that of height. It may be seen in table 2, that the height of non-inoculated plants was not consistently higher than inoculated plants of either resistant or non-resistant plants.

#### SMUT INFECTION IN FIELD PLANTS

A summary of the data of the field experiments may be found in tables 4 and 5.

Black Mesdag was found to be free from smut infection. Monarch and Gothland each developed three smutted plants in the inoculated series while the former showed four smutted plants and the latter two smutted plants in the non-inoculated rows. In these cases Monarch was infected by the covered smut while Gothland showed infection by the loose smut. In the experiment, however, Monarch had been inoculated with the loose smut while Gothland was inoculated with a race of the covered. An infection of four plants out of 300 may be considered as accidental and does not have any bearing on the results. *Avena brevis*, in-

oculated with a physiologic race of *Ustilago levis*, the covered smut, yielded a 17.4 per cent infection of the 287 plants surviving out of an original 300. Usually, this physiologic race of the Missouri smut collection yields a much lower percentage of infected plants. In 31 out of the 50 plants infected, only one or two lateral panicles showed infection. In,

TABLE 4  
Summary of field data

	BLACK MESDAG			MONARCH		GOTHLAND		<i>Avena brevis</i>	
	O*	L <sub>1</sub>	A <sub>1</sub>	O	A <sub>1</sub>	O	L <sub>1</sub>	O	L <sub>1</sub>
Smut Infection:									
Plants per row	0	0	0	0	0	0	0	0	4.2‡
Panicles per row	0	0	0	0	0	0	0	0	6
% infection	0	0	0	0	0	0	0	0	16.7
No. of plants	300	300	300	300	275†	300	300	300	300
No. maturing	281	297	285	262	239	287	287	287	287
Percentage maturing	93.6	99.0	95.0	87.3	86.9	95.6	95.6	95.6	95.6
Surviving at three days	290	298	292	274	250	296	294	289	287
Percentage surviving at three days	96.8	99.3	97.3	90.1	91.0	98.7	98.0	96.3	95.6
Yield of grain per plant (grams)	5.9	5.9	5.8	5.7	7.0	4.6	5.2	1.6	2.4
No. of culms produced	4.7	4.9	5.1	6.6	7.0	6.3	6.7	11.2	12.2
Height of plants in cm.	84.3	85.9	87.4	73.9	74.3	77.3	78.8	78.2	80.8
Date of first heading	6/16	6/14	6/15	6/28	6/29	6/15	6/16	7/2	6/29
Date of full ripening	8/1	7/29	8/1	8/5	8/6	8/3	8/3	8/12	8/13

\* O—Non-inoculated.

A<sub>1</sub>—Inoculated with the Missouri race of *Ustilago Avenae* Race 1.

L<sub>1</sub>—Inoculated with the Missouri race of *Ustilago levis* Race 1.

† 25 plants of the original 300 lost due to drowning in constant temperature tank.

‡ All smutted plants in this series are tabulated in Table 5.

only five of the 50, however, was the main panicle infected. It was possible therefore, to choose plants in which the presence of the mycelium was a certainty. The yield, height and production of culms in these 31 plants with a laterally infected panicle are shown in table 5. It may be readily seen that these plants with a sporulating infection compare favorably with the non-inoculated plants.

#### SURVIVING FIELD PLANTS

The smut fungus did not affect the survival of the resistant plants. In Black Mesdag, 95.6 per cent of the seed inoculated with *Ustilago Avenae* produced mature plants as compared with 93.6 per cent maturation of the non-inoculated plants, while 99 per cent of the seed inoculated



with *Ustilago levis* were brought to maturity. In Gothland, 95.6 per cent of both the inoculated and uninoculated plants survived. In *A. brevis* 95.6 per cent of the inoculated plants matured as compared with 93.6 per cent of the non-inoculated. Of these inoculated plants 50 out of the 287 surviving were definitely smutted. In Monarch 86.9 per cent of inoculated plants matured as compared with 87.3 per cent of the non-inoculated

TABLE 5

*Smutted plants of Avena brevis inoculated with U. levis*

1 LATERAL PANICLE SMUTTED				2 LATERAL PANICLES SMUTTED			
PLANT NO.	YIELD GRMS.	HEIGHT CMS.	NO. CULMS	PLANT NO.	YIELD GMS.	HEIGHT CMS.	NO. CULMS
1	3.4	85.3	13	16	2.0	86.1	14
2	2.3	82.2	11	17	3.2	87.8	15
3	2.8	80.1	12	18	2.1	79.2	13
4	3.2	87.9	7	19	2.5	75.3	12
5	2.4	78.2	13	20	1.8	87.2	9
6	3.0	84.1	15	21	2.5	81.3	14
7	2.5	80.0	12	22	2.7	79.2	15
8	3.3	79.2	14	23	2.6	79.3	15
9	3.6	78.1	18	24	2.6	76.2	13
10	3.6	89.1	17	25	2.5	84.7	12
11	2.3	75.3	16	26	1.9	80.1	11
12	2.1	77.2	9	27	2.0	77.2	20
13	1.7	78.1	10	28	3.1	87.9	16
14	3.0	80.0	11	29	2.6	88.3	12
15	2.4	83.1	12	30	2.3	70.6	7
				31	2.7	72.1	9
Av.	2.8	81.2	12.7		2.4	80.7	14

The average of the same characters in the non-inoculated plants is:—

Yield, 1.6—Height, 78.2—No. of culms per plant, 11.2

plants. It is to be noticed, however, that an average of about 3 per cent of the plants were lost three days after transplanting. This may have been due to a heavy storm which caused some damage by breaking the leaves of some of the young plants. From these data, it may be seen that inoculation with smut spores did not adversely affect the survival of plants thus treated.

#### YIELD OF GRAIN

It is readily seen that inoculation with smut spores did not adversely affect the yield of resistant varieties of oats. In fact, except in Black Mesdag, the data indicate that the inoculation produced a slight stimulation in yield. However, it is not deemed advisable to draw such a conclusion since the differences are variable and, except in the case of Mon-

arch, are not large enough. It is interesting to note that the yield of the 31 laterally infected plants of *A. brevis* was greater than that of the non-inoculated plants.

#### HEIGHT OF PLANTS

The plants of both inoculated and non-inoculated rows may be said to be about the same height (table 4). In some averages, the inoculated plants are shown to be taller by two centimeters. However, with the error present in such measurements of height, the differences are not important.

#### HEADING AND RIPENING

There was little or no difference between the heading and ripening dates of the inoculated and uninoculated plants of each oat variety as shown in table 5.

#### SUMMARY AND CONCLUSION

The oat varieties of *A. sativa*, namely Black Mesdag, Markton, Scottish Chief, Early Champion, Gothland, Monarch and of *A. byzantina*, namely Fulghum, and strains of *A. strigosa* and *A. brevis* were grown for a period of a year to test the hypothesis that covered smut (*Ustilago levis*) and loose smut (*Ustilago Avenae*) present as a non-sporulating infection may affect resistant varieties.

All seed in this study was dehulled and examined for injury before use in the experiments.

Data derived from an examination of 880 greenhouse plants and 2700 field plants show that varieties resistant to various physiologic races of loose and covered smut are not injuriously affected by inoculation with such smut. The yield, height, number of culms per plant were not affected. Neither was there any difference in the dates of heading and of ripening between inoculated and non-inoculated plants of each oat variety.

Cytological investigation of inoculated resistant plants shows that the mycelium is present in varying percentages in the coleoptile but penetrates no further. In inoculated non-resistant varieties the mycelium penetrates rapidly to the growing point where it is found at about thirty days after inoculation. This confirms the work of Kolk, (1930) who made similar observations on Black Mesdag, a resistant variety, and on Victor, a susceptible variety. This coleoptile infection of the resistant plants does not appear to have any adverse effects on the height, yield of grain, production of culms and heading and ripening of these plants.

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## Fasciation and its relation to problems of growth

### II. Changes from the fasciated to the normal state, with a discussion on the nature of the shoot

S. C. BAUSOR

(WITH 58 FIGURES)

In *Phaseolus multiflorus* the fasciated state of shoots which arise in the axils of the cotyledons after decapitation is transitory and unstable. Characteristic changes, especially in the nature of branching, are produced by progressive apical growth which finally give rise to cylindrical structures. The different processes by which a change of state is brought about will be discussed from the point of view of gross morphology, followed by an histological description of the cellular changes which accompany them. From the data assembled in these connections inferences will be drawn as to the morphological significance of fasciation and as to the ultimate nature of the shoot.

Previous investigations on the morphology of fasciation were mainly concerned with its mode of origin. These led to the formulation of two contrary views. The first proposed that it resulted from fusion of two or more stems or other cylindrical organs in a single plane in the early stages of development; the second, that fasciations resulted from unusual growth in a single meristem.

In 1751 Linnaeus summed up fasciation as a fusion of many stems which were borne in crowded quarters, and listed ten plants in which it occurred.

Hincks (1853) suggested that such fusions took place as a consequence of superabundant nutrition following a check in growth which produced numerous buds in close proximity. This interpretation was contrary to the opinion of Moquin-Tandon (1841) who suggested that only a single axis was involved, which became flattened by a peculiar manner of growth.

Masters (1869) classified fasciation as a phenomenon of cohesion and disputed Moquin-Tandon's arguments as follows:

(A) Although normally single-stemmed plants like *Androsace*, *Primula*, etc., may fasciate, such plants not infrequently produce several distinct stems; (B) the majority of fasciated stems have an increased number of leaves and buds; (C) in some cases the tissues of fasciated stems are organized into two steles, each with a distinct pith; (D) although it was considered unlikely that fusions should take place in one plane, nevertheless, the buds may be formed in one plane at the start,

and be of the same age; (E) leaf arrangements of fasciated stems sometimes show fusions of several spirals or whorls.

Sorauer (1909) also considered fasciations as resulting from a single meristem. He based his conclusions on the unity of the mature fasciated structure and upon the fact that the leaf divergence in fasciated *Picea* forms a continuous spiral.

A compromise explanation was proposed by Worsdell (1905). According to him, fasciation arose through the failure of the lateral branches and leaves to dissociate from the axis on which they were borne, and not through cohesion of distinct axes. Nicolas (1928) considered this merely as a special view of the fusion hypothesis.

Davies and Bennett (1929), describing a case of fasciation in *Ailanthus*, speak of the phenomenon as "abnormal branching," and not as fasciation. Many others reporting on fasciation descriptively have adopted one or the other of these views. However, since such questions cannot be settled by a consensus of opinion, further citation will not be made at this point.

All of the above opinions were based upon the appearance of mature fasciated structures.

Nestler (1894a) first investigated the problem histologically in embryonal tissues of the fasciated stem. Comparing normal and fasciated apical meristems, he came to the conclusion that there was no evidence in support of the contention that fasciation arose from fusions. On the other hand, he found that plants with a conical meristem in the normal state possessed a flattened apical comb in the fasciated condition (*Veronica longifolia*, *Crepis biennis*, *Aconitum Napellus*, etc.), and that plants which normally had a single apical cell possessed a line of apical cells when fasciated (*Cryptomeria japonica*).

Recently, by a study of the early stages of fasciated development in *Quercus rubra* and *Q. pedunculata* and in *Phaseolus multiflorus*, Georgescu (1925, 1927) concluded that fasciation arose from the fusion of many buds. He postulated that intercalary growth in the cushion of tissues formed by the development of secondary axillary buds resulted in fasciations.

Actual proof of these opinions is difficult because of discontinuous observations. The meristems are too small actually to be observed during their development, and when a meristematic region destined for a lateral branch fails to separate while in the embryonic state from a similar meristematic region which represents the normal apex, the distinction between fusion due to failure of dissociation and the flattening of a single meristem disappears. It is conceivable that both methods may de-

terminate the fasciated state in the same or different plants under different circumstances.

In his discussion of phylloclades which are flattened axial structures of limited growth, Velenovský (1907) in a footnote, pointed to the resemblance between these structures of normal occurrence and the abnormal state of fasciation. In 1868 deCandolle, from a study of the vascular system especially, theorized that the leaf itself was really a branch with limited growth. It is at least suggestive, in the nature of the organization of the leafy shoot, that a fundamental principle of general biological significance underlies the organization of dorsiventral structures in vascular plants, whether in the normally occurring phylloclades, in the leaf, or the abnormal condition of fasciation.

The recently discovered fossil vascular plants from the Devonian has renewed interest in the controversy over the nature of the leafy shoot. Kidston and Lang (1917, 1920(a), (b), 1921) reported on three new genera of fossil plants which are among the earliest known vascular cryptogams. Two of these, *Rhynia* and *Hornea*, were entirely rootless and leafless. *Asteroxylon* was of more complicated organization. It was invested with small, spirally arranged leaves, with each of which a leaf trace was associated. The trace, however, extended only as far as the base and did not project into the free portion of the leaf.

Lang (1931) reinvestigating *Psilophyton* from Dawson's material of 1859 and also additional material from the Scottish Chert beds (1932), found that the leaves of this fossil were entirely devoid of vascular tissue and stomata. There is good evidence that these emergences were glandular, and not "assimilatory" in function.

If plants similar to those of the early Palaeozoic be assumed ancestral to all other vascular plants, the leaf (megaphyll) must necessarily have been of secondary origin. The evidence to date points to this as being the case, as was indicated by Halle (1916). "The most obvious negative characteristic of the Rörögen (Lower Devonian) Flora, and according to Dawson, also of the Gaspé flora, is indeed the absence of any fern-pinnules or other foliar laminae. On the other hand there occur abundantly remains which might well be held to be rachises or fern-fronds or their branches, were it not for the absence of any traces of laminae." Substantiating data supporting the theory of the secondary origin of leaves, at least in plants of Psilotalean alliance, was furnished by Holloway's (1921) study of the embryology of *Tmesipteris*. The embryo is devoid of cotyledons, and the young sporophyte is a leafless rhizome with apical growth, upon which branches may originate adventitiously. The leaves first appear upon aerial branches back of the growing apex.

The origin of the leaf is the next question raised.

Bower (1884) illustrated the similarity in mode of branching between the leaf and stem but was not at that time fully prepared to accept a homology between them. Tansley (1907), from analyses of fossil and extant ferns, hypothesized that the large fern leaf was a modified branch system, and that the microphylls were reduced branches. Lignier (1908) proposed that the large fern leaf arose by unequal dichotomy of an originally cylindrical organ (caulome), the weaker branch of which became appendicular. Later by cladodification of the ultimate branchlets the first pinnule came into being. He believed the microphylls arose in a different manner. The caulome was clothed with emergences (phyllome) as in *Psilophyton*, which were later modified into microphylls.

Bower (1908) put forward his strobiloid theory in which he contended that the first leaf arose as an emergence (compare this with Lignier's phyllome) from the surface of the sporophyte. These, it was postulated, were from the first sporophylls, since they arose in connection with isolated sporangial masses. Microphylls were derived from this primitive leaf by modification.

In contrast to the above, there have been workers who postulated that the leaf was the primitive organ, the stem having arisen secondarily. Thus, the shoot has been considered as a structure of composite nature of which the leaves were the chief components.

Gaudichaud (1841) divided the shoot into units which he termed phytons, each consisting of four parts, blade, petiole, portion of the stem, and root. Thus, the whole plant was made up of a number of independent units. This theory was discredited as being based upon inaccurate anatomical data. However, Chauveaud (1921) showed that a similar system could be worked out from embryological facts which probably are sound. He established a shoot-unit to which he applied the name phyllorhize, since it consisted only of root and leaf. Upon the leaf a meristematic initial formed, which developed into a root, leaf, and another meristematic initial. In this way the plant was continually being built up. The foliar tissue between the initial and the root of each unit formed a stem or axial segment.

Campbell (1921) likewise showed that the steles of the leaf and the root developed previous to the initiation of the stem in the *Ophioglossales*.

Celakovský (1901) proposed a somewhat different shoot-unit which consisted of a leaf and a sector of the stem extending vertically downward from it to the leaf directly below it. Priestley (1929) added further evidence to bolster this shoot-unit. He showed that the distinction be-

tween node and internode was not a natural classification, that in development the leaf traces developed downward past the node to the leaf directly below it, and that, furthermore, the cells were in different physiological states in different sectors of the node. He spoke of the shoot as "organized as a community of tissue aggregates." Schoute (1931), in a critique on phytonism, showed that Celakovský's unit could be explained in other ways.

The different theories which have attempted to divide the leafy shoot into integral units are not without some basis of fact. It seems to me, however, that these units should not be looked upon as morphological entities, but rather as physiological units, or areas of localized growth.

The most logical view point, crystallized from the whole of the data on this subject, has been summarized by Bower (1935) "... the axis and the leaves act together as a physiological whole and are so initiated in embryology; also in evolutionary history, as based on comparison of early fossils such as the Psilophytales. The shoot-unit of Sachs is the natural, that is, the evolutionary unit."

#### OBSERVATIONS ON THE GROSS MORPHOLOGY OF THE FASCIATED SHOOT

Orderly reorganization of the fasciated shoot into a structure with cylindrical internodes can take place only where the tissues are in an embryonal state, since rigidity of the plant cell-wall prevents alteration of form, except that inherent in the elasticity of the wall material. However, drastic changes which result in more or less cylindrical structures sometimes do occur in mature fasciated organs. These take place through fissures sometimes followed by splitting, or by atrophy of a part of the fasciated stem. Such changes never lead to permanently normal stems, they merely diminish the already existent fasciated state.

*Fissures.* When stresses become unbalanced, the fasciated structure suffers violent splitting and lacerations of varying size. In some instances horizontal notches are produced singly, or in a series. If the wound occurs near the base of the stem at an early stage of development, the elongation of the internode which follows, widely separates the torn tissues which were formerly in contact (fig. 56, A and B). This results in raising the severed part some distance above the original cleft. The amount of internal surface exposed by the breach thus increases as the stem elongates, producing long vertical wounds. In the two cases shown in the photographs it will be noted that the remainder of the stem which is still functional is almost cylindrical.

In other cases, older stems split as a result of unequal tensions on two sides. Figure 56, C, shows a case where the split took place in such a



way as to render almost cylindrical the portion of the stem which was still in continuity with roots and stem apex. Fissures frequently are found on fasciated petioles.

The amount of fasciation is always reduced when splitting occurs,

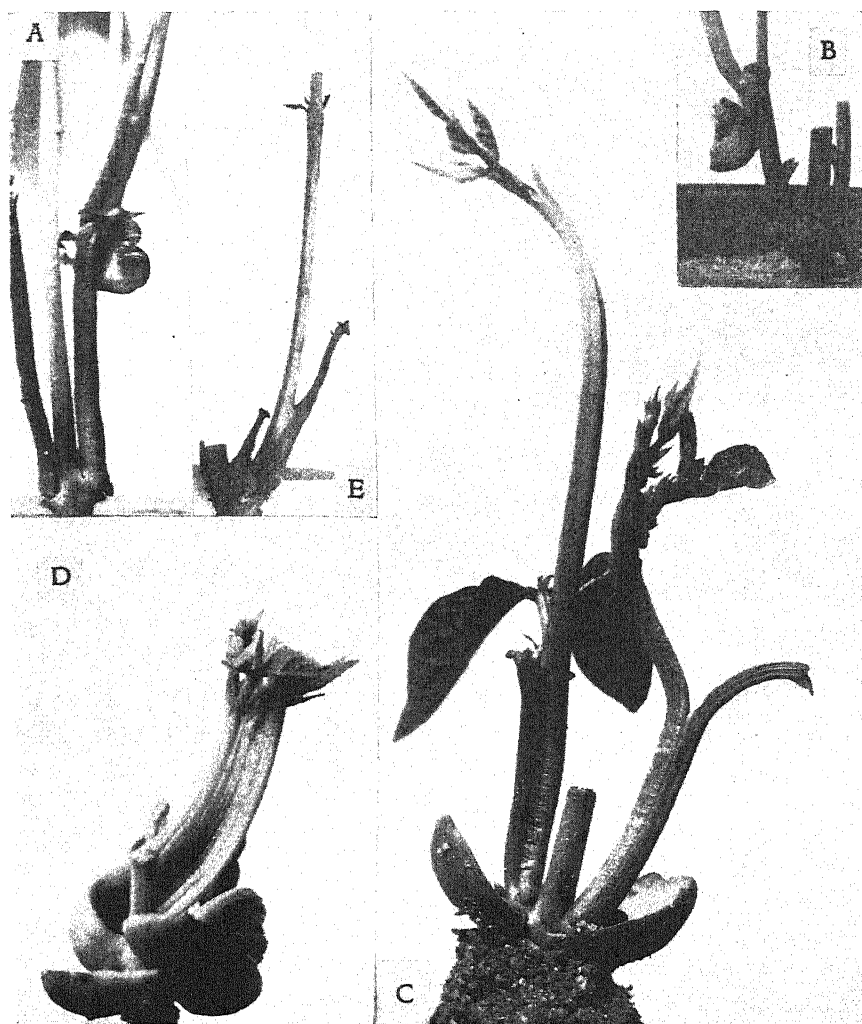
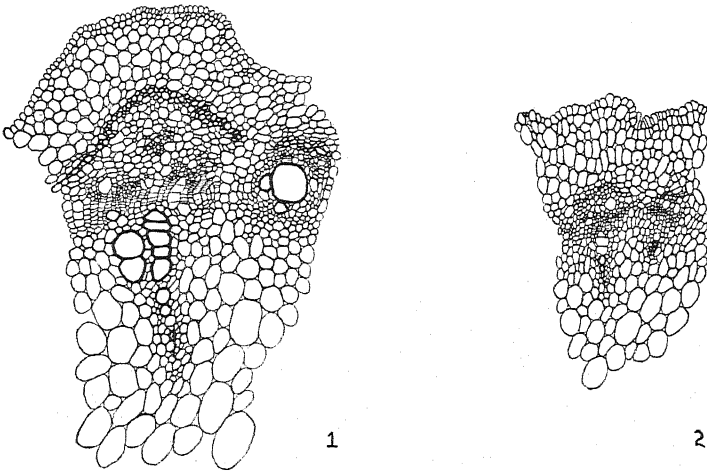


Fig. 56. Secondary alteration of the fasciated condition in maturing organs, showing: A, B, the separation of tissues through the elongation of the internode; C, the axillary shoot on the right, with a large split. Several horizontal notches are shown above. D, the right hand fasciated shoot has split; E, a shoot in which the abaxial sector has atrophied. These phenomena reduce the fasciated state, and in many cases produce almost cylindrical structures.

but the effect is only of local significance. The tissues above the wounds are still fasciated and, as far as it was possible to determine, they did not seem to affect the growing regions which were evolving more fasciated structures.

That the fissures resulted in the formation of cylindrical stems was not entirely due to chance. The adaxial portion is usually better developed than the rest of the fasciated stem, rounding out into a more or less cylindrical sector, while the abaxial sector is usually elliptical and poorly developed. There are, however, all gradations in these fasciated



Figs. 1 and 2. Explanation in the text.

axillary stems, from a condition in which the sector is elliptical in outline, with tissues equally developed, to very pronounced cases of unequal development, as just described, with the adaxial tissues much in advance of the tissues of the rest of the stem. When splitting occurs it usually separates the two unequally developed regions.

*Atrophy.* The tissues of the flattened portion of such unequally developed sectors are composed of smaller cells in which differentiation is lagging behind that in the enlarged adaxial portion. The difference is particularly evident in the vascular development and secondary growth. In figures 1 and 2 are two bundles from opposite sides of the long axis of a cross-section. The bundle (1), located on the adaxial side, has larger and more metaxylem cells and the protoxylem has already been crushed. The cambium is well developed. The smaller bundle (2) has but a few small metaxylem elements and functional protoxylem, while the cambium has just begun to form. This is a sectorial dwarfing. The dif-

ferences are quite evident in the more mature plant. When about a month old the elliptical portion of the fasciated stem becomes completely atrophied in some cases, appearing to be decayed. It becomes brown and flaccid in contrast to the green and turgid "cylindrical" adaxial portion. Stems with such differential development are physiologically cylindrical, since most of the translocation presumably takes place on the adaxial side, probably just as though the other part were absent (fig. 56, E).

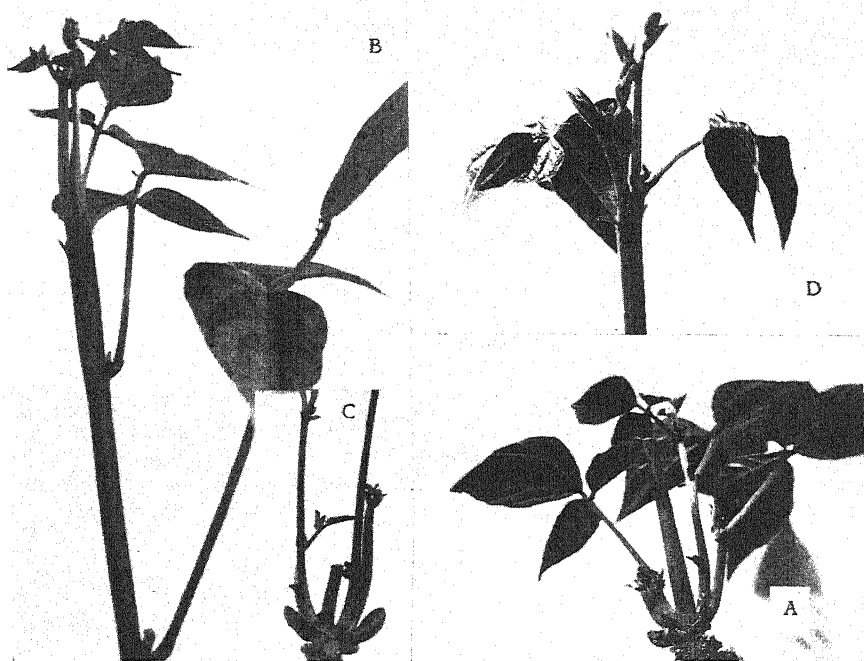


Fig. 57. Bifurcation. A, C, forking near base of stem. Both branches are normal. B, bifurcation at a considerable distance from the base of stem. One branch is normal, the other fasciated. There is a normal leaf on the flat side just beneath the fork. D, both branches resulting from the bifurcation are still fasciated. There is a fasciated leaf on the flat side just beneath the fork.

The production of fissures and the atrophy of a sector of the fasciated stem were the only means observed by which a fasciated structure, which had already differentiated, returned to normal shape or became less fasciated.

On the other hand, forces acting upon the fasciated apical meristem or meristematic regions lead to orderly reorganization of the mass of cellular components, resulting in the eventual formation of normal

cylindrical, or nearly so, leaf-evolving axes. From this stage onward the fasciated plants are similar in all respects to the normal. This phase of the development of fasciated axillary shoots in which the abnormal state is lost has not been sufficiently emphasized. Of all the variables associated with fasciation in *Phaseolus multiflorus* this is the most constant feature. The fasciated shoot always returns to normal, and usually at a very early stage in development. Apical reorganization results in the establishment of special regions, the development of which differs in rate and kind of growth.

*Forking of the fasciated stem.* Bifurcation is a very common result of reorganization of fasciated shoots, although a very unusual method of branching in the Angiosperms (where branching is normally lateral and not apical). The two branches are always smaller than the original axis from which they arose and they are always less fasciated since they divide the longer axis of the fasciated stem (fig. 57, A, B, C.).

There is some evidence that the two daughter branches, each produced as an organized cauline structure, are composed of equivalent amounts of cellular elements which before bifurcation were organized as a single structure. At a very early stage of bifurcation the sum of the diameters of the two bifurcated branches approximately equals the longer diameter of the fasciated parent stem before the forking took place. The same relation holds, even in older, more mature structures, indicating that subsequent growth was of the same nature in particular cellular masses whether organized as a single entity—as it is below the fork—or as two independent entities, as in the branches.

In one plant the longer axis of the fasciation, three millimeters below the fork, measured 6.1 mm., while in the same axis the two branches were 3.1 and 2.5 mm. long, respectively, measured three millimeters above the fork. At the fork, the diameters of the two branches were 3.2 and 2.2 mm. long, and the undivided stem immediately below was 5.7 mm. In a second plant similarly analyzed, three millimeters on either side of the fork the branches measured 2.2 mm., and 3.0 mm., and the parent stem 4.9 mm., while at the fork they were 1.9, 2.6, and 4.5 mm., respectively. In a third plant, the branches measured 1.7 and 1.8, respectively (at three millimeters distance from the fork); the parent stem 3.8 mm. At the fork the branches were 2.0 and 2.0, and the parent stem was 4.0.

The sum of the branches produced by bifurcation thus approximately equals the parent structure from which they came.

In this connection, deVries (1894) found in a fasciated plant of *Crepis biennis* which produced six unequal branches, that the sum of the diam-

eters of the branches was approximately equal to the diameter of the fasciated stem from which they arose.

A leaf is often, but not always, borne on the flat side of the fasciated stem below the bifurcation (fig. 57, B, D).

*Leaf-sectoring.* The fasciated state very often is considerably reduced or entirely disappears in connection with the production and development of foliar organs. The shape of the stem approaches the normal cylindrical above the nodes of the leaves in question. It appears in the mature state as though a sector of a mass of cells which previously had differentiated as a component of the fasciated stem, developed into leaves or leaf-like organs and their axillary buds. The term leaf-sectoring has thus been given to this phenomenon. The process suggests a differential development of sectors of the meristem, one or more of which become determinate structures and take no further part in the development of the mature plant.

Leaves developed in this way may be normal or fasciated, opposite or alternate, and the sectors of the meristem from which they arose may be lateral or median. Fasciated stems returning to normal through the divergence of large leaves with fasciated petioles and numerous leaflets are illustrated in figure 58, A, B, C. The leaf is laterally situated relative to the rest of the stem, as it is normally. In D, a similar reduction occurred through the formation of a large fasciated leaf, the position of which, however, is median, with a small normal stem to one side, and a bud to the other side of it. Below the small normal stem and in the same plane, is a stipule in the axil of which a bud has only partly developed. The stipule has not greatly altered the fasciation. This plant is so very abnormal that caution must be used in proposing an interpretation. The fasciated "leaf" is itself complicated, and appears as a combination of foliar and axial organs. The whole structure, however, is determinate. There is a pulvinar region 0.5 cm. from the base of the fasciated petiole on the adaxial side which can be seen in the photograph, but there is no such region for the rest of this structure.

When fasciated leaves are borne on the side of the shorter diameter the stem apparently is affected little or not at all (fig. 57, D). In this instance the fasciated stem is reduced by bifurcation above the insertion of the fasciated leaf on the flat side of the stem. It will be noted that this leaf does not play any direct part in the reorganization of the shoot. The normal trifoliolate leaf to the right of the stem, slightly above the bifurcation, however, does reduce the right hand branch to cylindrical shape. The left hand branch of the bifurcation is still fasciated above the fork. It, too, becomes normal above the first node. Thus, in this plant,

there are two different factors which finally result in the development of cylindrical axes characteristic of normal plants: first, bifurcation; and second, sectorial reduction through the development of leaves.

Fasciated leaves are sometimes borne by stems which in other respects appear normal. In one case the main shoot, the epicotyle, which was slit near the base instead of decapitated, bore a pair of opposite unifoliate leaves at the first node, a trifoliate leaf at the second, and a fasciated leaf at the third, and normal trifoliate leaves at the fourth and fifth nodes. All the internodes were normal.

Fasciated structures of foliar nature which reduce the fasciated state of the stem may have originated differently from those which do not take such a part, although they appear similar in gross morphology. The former appear as structures derived from the incorporate cauline elements, from a mass of cells corresponding in position to a similar mass which in the previous history of the shoot became embodied as a component of a stem, while the latter appear as lateral outgrowths from the main body, similar to normal leaves.

Other cases of the reduction of the fasciated state to the normal through leaf-sectoring are shown in figure 58, E, F. The shoot in E returns to normal after the production of two normal leaves, which are almost oppositely arranged; that in F after the production of a single normal leaf.

#### THE HISTOLOGY OF THE TRANSITION OF THE FASCIATED SHOOT

*Changes due to fissures.* A brownish scab of corky appearance, composed of crushed, dead cells, covers over the tissues which were exposed by naturally occurring fissures and splitting. Beneath this a periderm forms. The new walls laid down by the dividing parenchyma cells which give rise to the periderm are more or less parallel to the wounded surface. When the wounds are small and do not penetrate the stele, the outermost layer of living cortical cells divides to initiate the periderm; in deeper wounds not only does the first row of living cells divide, but also several rows behind it, not necessarily contiguous. In one case the cells near the center of the pith were dividing, although the wound extended only to the stele.

Cicatrix formation was not studied in further detail.

*Changes accompanying bifurcation.* The critical change incident to bifurcation is the reorganization of the single fasciated stele into two independent vascular systems shortly before the physical separation of the stem into two branches. A furrow, which becomes progressively deeper up to the place of the eventual forking, precedes the division of the stele.

This narrowing is obviously associated with a decrease in the number of cells in the pith, which now become stretched at right angles to the axis

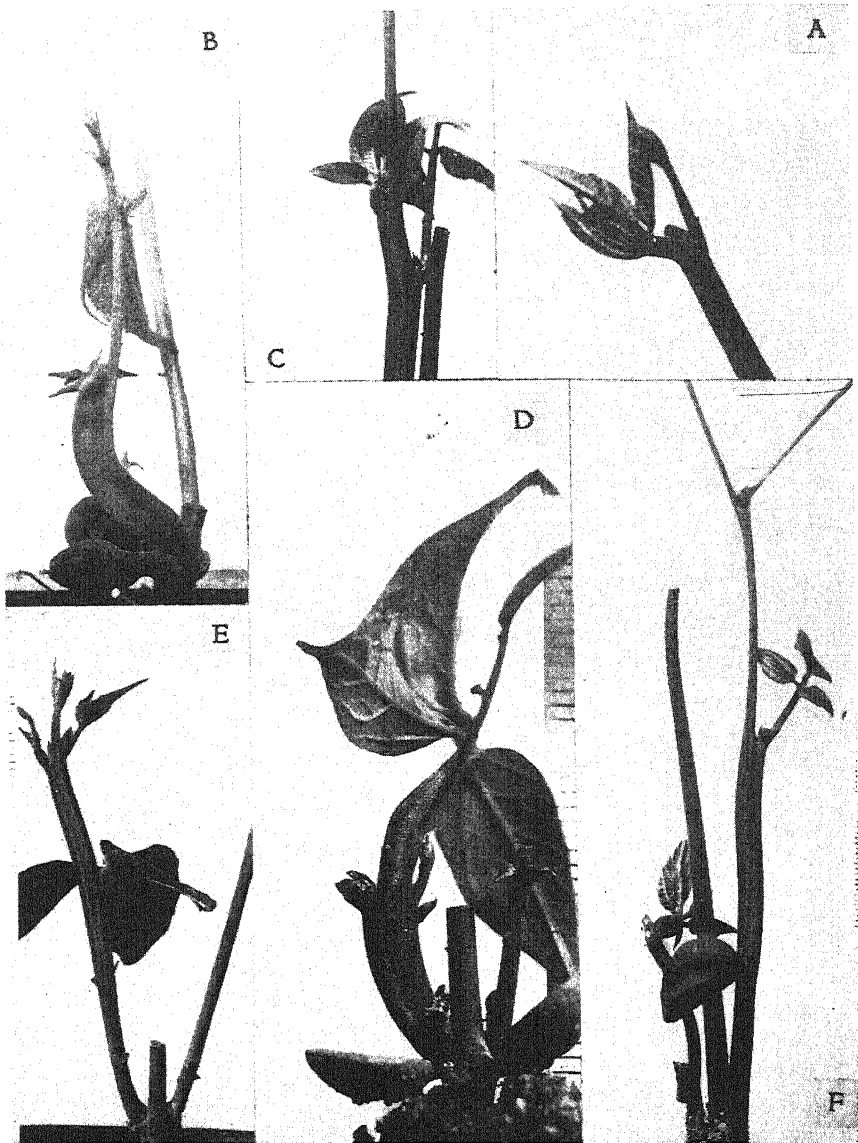


Fig. 58. A, B, C, three examples of leaf-sectoring in which a fasciated leaf is laterally situated. D, a median leaf with a bud at one side and a small normal shoot on the other side of the leaf. E, F, fasciated shoots reduced to normal by the production of normal leaves: a pair of almost opposite leaves in E, a single leaf in F.

of the stem. The vascular bundles present in this region also change their direction, running diagonally in the pith, later either to resume their vertical direction as a bundle of identical structure on the outskirts of the furrowed region, or to be reorganized into a new bundle outside of the furrow through branching and anastomosing with other bundles, or with metaxylem elements in the fiber ring. The elements of the fiber ring on opposite sides finally converge, their course being at first diagonal, then horizontal, at which time their position is directly above the horizontal pith cells. At this stage the pith of the stele is separated into two parts by the fibers. The fibers then take a diagonal course away from the narrowed region, diverging to opposite ends of the longer diameter of the fasciated stem, and finally run vertically. Two steles are thus completely organized, separated from each other by an isthmus of parenchyma tissue in the narrowed region. The essential feature in the reorganization of the original fasciated stele into two steles is the alteration of the direction in which the cells stretch, accompanied by a diminution in the number of cells, especially those in the center of the stem, presumably by omission of certain cell divisions in this region.

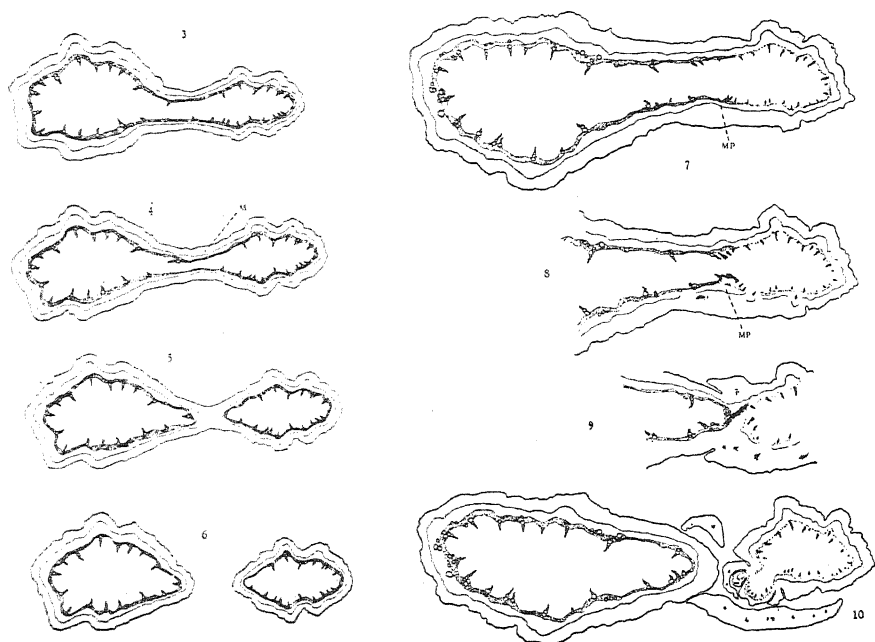
The rest of the tissue differentiations in the stem—those outside of the region of the furrow—remain unchanged during the formation of the two steles and they persist in the daughter branches as they were when arranged in the single structure.

In the simplest case of bifurcation observed (figs. 3–6) all vascular bundles which were present in the undivided fasciated stem persisted unchanged in the two branches. The other tissues, and also the contour of the stem, were approximately the same in the branches as they were before forking took place, but in most cases could not be as easily traced as the xylem differentiations. In this fasciated stem, before bifurcation, there were 33 primary bundles, and two metaxylem elements in the fiber ring (fig. 3). During the reorganization of the stele into two parts, a new metaxylem element formed in the ring (figs. 4 and 18) and bent diagonally, anastomosing with a bundle in the narrowed region. Its full length was approximately 255 microns (17 sections cut at 15 microns). The bundle then passed to the left at a slight angle away from the furrow, and became incorporated into the larger stele (fig. 5).

Superposing the original drawings of figures 3 and 5 one on the other, the chief difference in contour of the stem was merely the slight narrowing in the isthmus of tissue separating the two steles. It was also obvious from the drawings that the local differences in contour persisted in the fasciated stem before and after the two steles were formed and also after the separation of the stem into two branches. Comparing figures 3, 4, 5,



and 6, it will be noted that there are several comparable points in the general outlines: to the left a flat side, opposite which are three vascular bundles; a ridge on the top, opposite which is a single bundle; and a fur-



Histology of fasciated shoots in the region of bifurcation (figs. 3-27) and in the region of leaf-sectoring (figs. 28-55). The stippling represents the fiber ring, the line outside of it the endodermis. The mesophyll of leaves is represented by cross-hatchings.

Figs. 3-6. The fasciated stem (3); the narrowing occurs, a new metaxylem element (M) appears in fiber ring (4), shown in detail in fig. 18; two steles organized, separated by an isthmus of parenchyma (5); separation of the branches (6). The sum of the bundles in the two branches is equal to that of the parent stem, and the contour of the parent stem persists in the branches.

Figs. 7-10. The fasciated stem (7); a metaxylem element anastomosing with one of the primary bundles (MP), three traces also are shown on the lower side, two are just leaving the stele (8); the fibers have converged as two primary bundles from the upper side together cross the furrow to the opposite side. A single trace is shown in the stipule on the upper side, and of the three on the lower side, one has branched (9). The two branches show persistence of vascular differentiation and contour as in the parent stem.

row on the lower side of the drawings, also with a single bundle opposite it. To the right there are two ridges on the upper side and two on the lower side, all of which can be matched in all four figures, even after branching. There are 16 primary bundles in the larger branch corresponding to 16

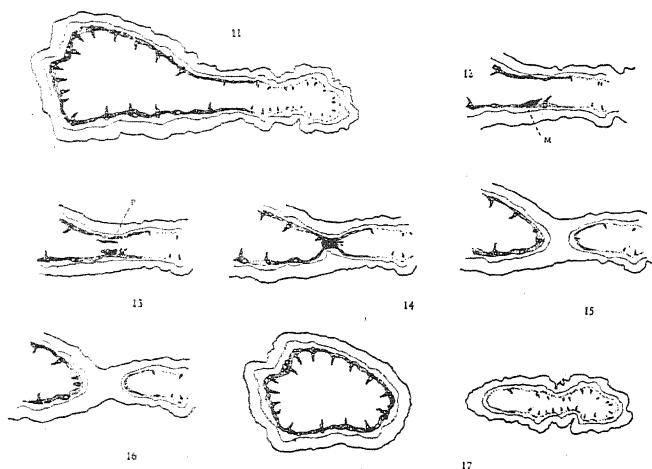
of the 33 in the fasciated parent stem, and there are 17 primary bundles and two metaxylem elements of the fiber ring in the smaller branch, corresponding to the remainder in the parent stem.

A second example of a bifurcating fasciated shoot in which a new bundle originates in the pith of the furrowed region is illustrated by drawings of serial sections in figures 11-17. The fasciated stem has 37 primary xylem bundles, of which but a single one is affected during the reorganization of the stele. A metaxylem bundle to its left (fig. 12) becomes horizontal and anastomoses with it, at about the same time that the pith bundle makes its appearance (fig. 13). The primary bundle in question then branches as the fiber ring converges, a small branch in continuity with the protoxylem of the original bundle passing over to one of the newly organized steles, and the rest of the bundle remaining in the other stele. In figure 14 the horizontal fibers, together with the horizontal pith bundle, are shown separating the pith into two parts. After the complete separation of the two steles the smaller branch of the primary bundle anastomoses with the horizontal pith bundle, which does not continue vertically in this new stele, and as a consequence that region is devoid of xylem tissue (fig. 16) and it persists in the same condition after the physical separation of the two branches. The pith bundle does, however, become vertical in the other stele where it lies next to the primary bundle under discussion. After forking there are 16 bundles in the larger branch (of which one represents the pith bundle) and 22 in the flatter, more fasciated branch. There is, therefore, an increase of one bundle over the number in the parent stem before the reorganization of the stele.

The pith bundle resembles the other bundles of the stem in structure, being composed of spirally thickened protoxylem, and pitted metaxylem which is contiguous with the fiber ring. Its course is horizontal in relation to the long axis of the shoot, and it represents an apical bundle of the parent stem at the place where the stele is divided into two. Cut in longitudinal section the pith bundle would present the same appearance as do the vertical bundles in cross-section. All the primary bundles of the fasciated parent stem, except the one mentioned, remain unchanged. The contour of the two branches (fig. 17) is again similar to that of the fasciated parent stem. In the larger branch the prominent ridge corresponds to the prominent ridge to the left of the parent stem, figure 11. In the flatter branch the three ridges on the lower side and the ridges on the upper side and end of this branch correspond, with but slight changes, to those of the right hand sector of the parent stem.

In another bifurcating fasciated shoot the rearrangement of the

xylem elements of the furrowed region was more complex, and in addition, two stipules formed parallel to the longer axis of the cross-section of the stem. The rearrangement of the bundles at the narrowing region was independent of the departure of the traces to the stipules, although the two processes took place concurrently. There were 47 primary bundles in the fasciated shoot (fig. 7). As the stele was being divided into two separate steles a primary bundle anastomosed with a metaxylem trachea (fig. 8) and together they passed diagonally across the narrowed region,



Figs. 11-17. The fasciated stem (11); a metaxylem element (M), approaching one of the primary bundles with which it anastomoses (12); protoxylem of horizontal pith bundle (13-P); convergence of fibers separates pith into two parts. Metaxylem of pith bundle shown in black. The small bundle near the pith bundle is a branch of the primary bundle in fig. 12 (14); fusion of these two bundles (15); and their termination (16); parenchyma separating the two steles (15, 16); after branching (17). There is evident similarity in vascular differentiation and contour in figs. 11 and 17.

forming a bundle on the same side of the stem, but on the opposite side of the furrow. As this new bundle was assuming the upright position, a branch from it travelled back and united with two primary bundles which had anastomosed and crossed the furrow to the opposite side of the stem, there resuming a vertical position as a single bundle next to the first one. The fibers (fig. 9) converged at the furrow as this was taking place.

While the stele was dividing four bundles from the smaller, less mature sector departed from the stele into the cortex as traces for the stipules, three on one side for one stipule, and one on the other side for the second stipule (figs. 8, 9). After forking, the larger branch had 20 bundles (fig. 10),

of which 18 were identical with 18 of the original fasciated stem. The other two were the new bundles which formed from three primary bundles and one metaxylem trachea in the fiber ring as the two steles were being organized. In the smaller branch there were 22 of the original primary bundles.

The contour of the branches is again somewhat similar to the sectors of the fasciated stem from which they came. The larger branch, however, although having many points in common with the larger sector of the fasciated stem, is flatter than the latter. It is possible that this is due to

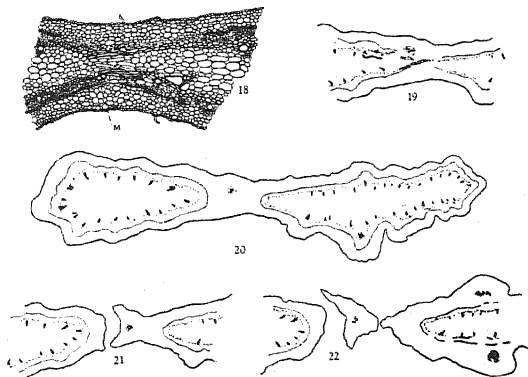


Fig. 18. Detail drawing of the narrowed region of fig. 4. A new metaxylem element (M) develops. Fiber and pith cells are stretched horizontally. There are fewer pith cells in the narrowest part than in the wider parts. This section precedes the convergence of the fibers which separate the stele into two parts.

Figs. 19-22. The convergence of fibers in such a way as to exclude one of the primary bundles (19); the bundle in the isthmus between the two steles (20); at the end of one of the branches, after forking (21); the separation of the emergence (22).

a crushing of the stem as it was sectioned. The outline of the smaller branch resembles that of the smaller sector of the fasciated stem on the upper side and end, but the rest of it is modified by the development of a bud (fig. 10).

Another case of rearrangement of the xylem elements preceding bifurcation is that in which the convergence of the fibers occurs in such a way as to leave one of the primary bundles outside of the newly formed steles (fig. 19). This bundle shifts to the isthmus of tissue separating the two steles, and after forking, is located at the end of one of the branches (figs. 20, 21). It functions as the trace of a stipule, or an emergence (since it is not associated with normal foliar development) which later separates from the branch (fig. 22). This structure is thus directly traceable to a

sector of the tissue of the isthmus and lower down in the stem, to stelar tissues which, in the original fasciated condition were arranged in such a way as to form a single unit structure.

Bifurcation is often accompanied by the formation of a leaf at the fork, but the process of reconstruction of the stele and the separation of the branches take place independently of foliar development. In this case, however, production of two steles is not accompanied by narrowing of the stem where the fibers converge; on the contrary, the presence of the leaf causes an increase in the size of the cortical region, an effect typical of foliar development.

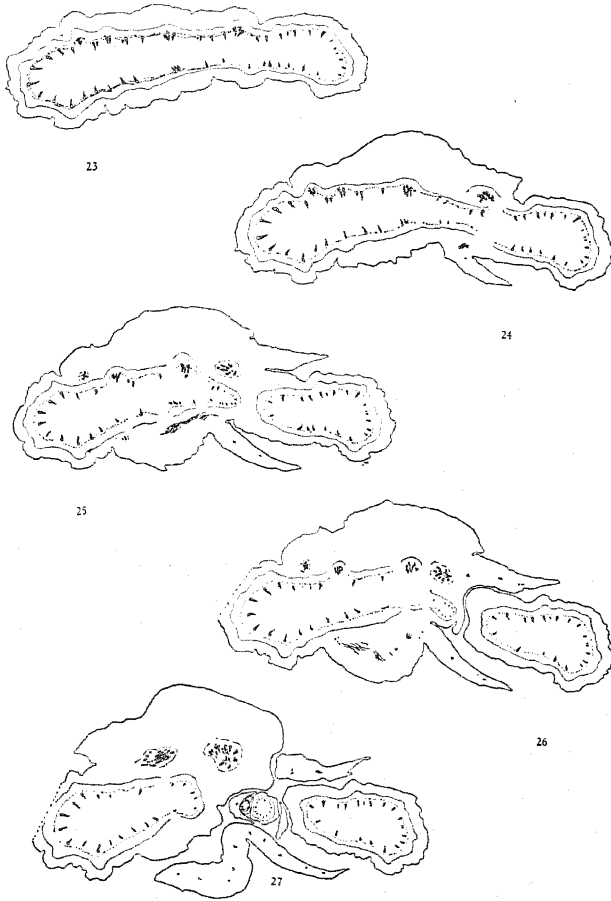
There are 55 primary xylem bundles, as shown in figure 23. As the pith is narrowing with the convergence of the fibers, four leaf traces are in the process of leaving the stele on the upper side (figs. 24, 25, 26) and a single trace on the lower side (fig. 24), followed later by two more (fig. 25), make the three which compose the xylem of one of the stipules. The furrow usually associated with the narrowing of the pith is obscured by the increased cortical development associated with petiole and stipule formation.

The fibers converge where the two traces on opposite sides of the stem have left the stele (right center, fig. 24). Three primary bundles are affected in the reorganization of the stele which apparently merely shift their position away from the converging fibers. After the separation of the two steles a bud forms at the end of the left hand branch (figs. 25, 26), followed by the production of a secondary bud (fig. 27). The primary bundles in the two branches of the bifurcation which were not affected by the production of leaf and stipules, nor by the bifurcation, persist as they were in the parent stem. The contour of a portion of each branch where it was not influenced by the leaf and bifurcation, has also persisted much as it was previously in the parent shoot.

The phenomenon of bifurcation may be considered a partitioning of a definite mass of cells, previously organized as a single structure, into two masses which together are approximately equal to the parent structure, both in its component cellular make-up, and in the differentiation of the cells. The shape of the branches when observed in cross-sectional outline also can be identified with the contour of sectors of the parent stem, except at the place of division of the stem into the daughter branches, or when the development of a leaf brings about secondary changes.

*Changes accompanying leaf-sectoring.* In leaf-sectoring, as in bifurcation, the important changes leading to a lessening of the fasciated condition involve a reorganization of the vascular tissues into two steles, followed by the production of two organs in place of the single stem. One

of the branches, like the parent stem, is indeterminate and continues the development of the plant. The other is determinate and foliar. In most cases of leaf-sectoring the division of the parent stem into two parts is



Figs. 23-27. The fasciated stem (23); four leaf traces on the upper side compose stele of petiole and stipules, three on lower side compose the stele of the second stipule (24, 25); two steles formed (25); separation of the branches and the formation of a bud lateral to the leaf (26); pulvinus of petiole forming, and an axillary bud (27). The contour is retained in parts of the branches corresponding to parts of the parent stem which are unaffected by development of leaf and stipules.

not mere partitioning, as was the general rule in bifurcation, but the sector of tissues involved in the construction of the leaf is increased by additional growth. The region at which stelar modification occurs is not

so small as that of bifurcation, and in most cases at least some of the bundles which compose the petiolar vascular system pass into the cortex as foliar traces. During bifurcation, on the other hand, the change in position of the xylem takes place through the pith.

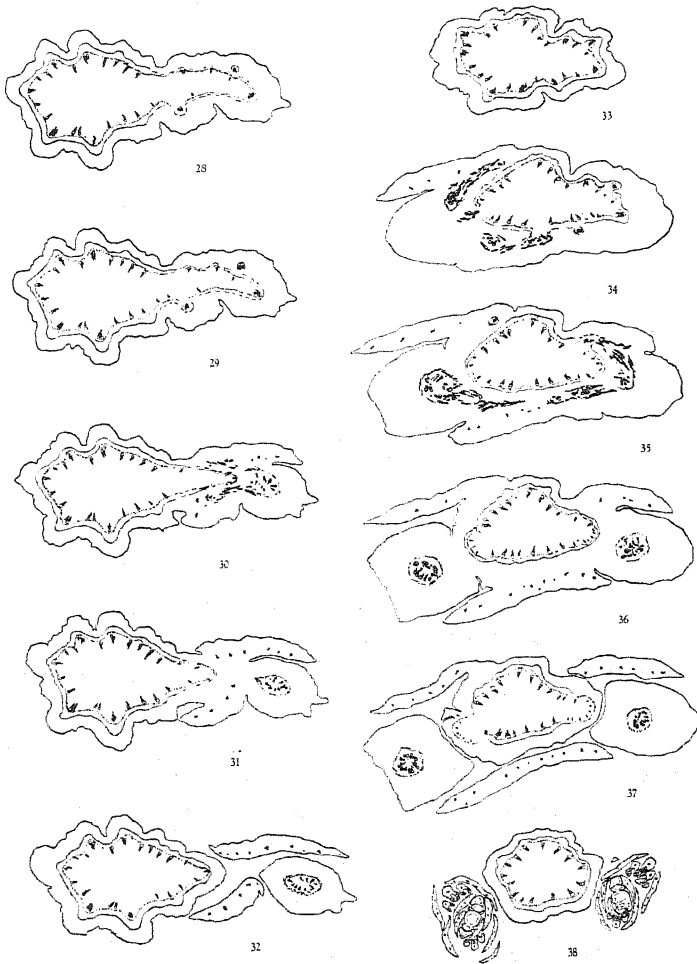
Types of leaf-sectoring: (1) In which a single normal leaf is involved. A fasciated shoot with 28 primary bundles (figs. 28-32) produced five traces in the abaxial sector, three on one side, one on the opposite side, and the fifth at the end of the stem. At this stage two new bundles appeared, so that 25 bundles remained in the parent stele. The four traces on the sides travelled longitudinally toward the abaxial end, branching *en route* to give rise to the vascular tissues of the stipules, one on each side of the stem. The five traces were then organized into the pulvinar stele, at the abaxial end of the stem (fig. 30). At the same time three bundles still remaining in the stele at the abaxial end were travelling in the pith diagonally away from this region toward the adaxial end, where they later became vertical. Two of them anastomosed on the way, but soon separated. The stele of the stem soon after became separate from that of the petiole (fig. 31). The former was now considerably smaller than before the separation of the leaf traces, for the stele now terminated around the three abaxial bundles which had shifted toward the adaxial end. The fasciated state was similarly reduced after the leaf and stipules were given off (fig. 32).

The contour of the stem above the divergence of the leaf was similar to that of the adaxial sector of the parent stem, but the outline of the abaxial sector of the fasciated stem previous to the departure of the traces was changed beyond recognition as the leaf developed. The shape of the petiole, however, seems to be identical with that of the abaxial end of the fasciated stem at the time the petiolar stele formed.

After the divergence of the leaf the stem had 24 primary bundles. One of the two which was previously noted to have anastomosed, having become smaller and smaller in its vertical course, finally terminated as the leaf diverged from the stem. The leaf was normal, and all the foliar xylem was in continuity with the stele through leaf traces.

(2) In which a pair of opposite normal leaves are involved. In another case (figs. 33-38) a pair of opposite normal leaves, with which eight traces were associated, was located on either end of the larger diameter of the fasciated stem. Three traces and a branch of a fourth formed the petiolar stele of one of the leaves, and another branch of the fourth, and the remaining four bundles formed that of the second leaf (figs. 33, 34,

35). Two axillary buds were associated with each of the leaves. Above the node, the stem was normal. In this case both leaves and axillary buds



Figs. 28-32. The fasciated stem (28); just before all five traces leave the stele (29); the traces forming the pulvinar stele and stipules (30); just before the divergence of the leaf (31); separation of leaf and stipules from the stem (32). Note the reduction of the fasciation and the persistent contour and tissue differentiation in the sector to the left, before and after leaf-sectoring.

Figs. 33-38. The fasciated stem (33); traces forming the steles of the opposite leaves (34, 35). Petiolar steles complete, leaves about to separate (36); separation of leaves and formation of axillary buds (37); separation of axillary buds (38). The stem is now normal.



appear as normal outgrowths, that is, as new tissue added to the shoot, and the assumption of a cylindrical shape in the stem above occurred very abruptly.

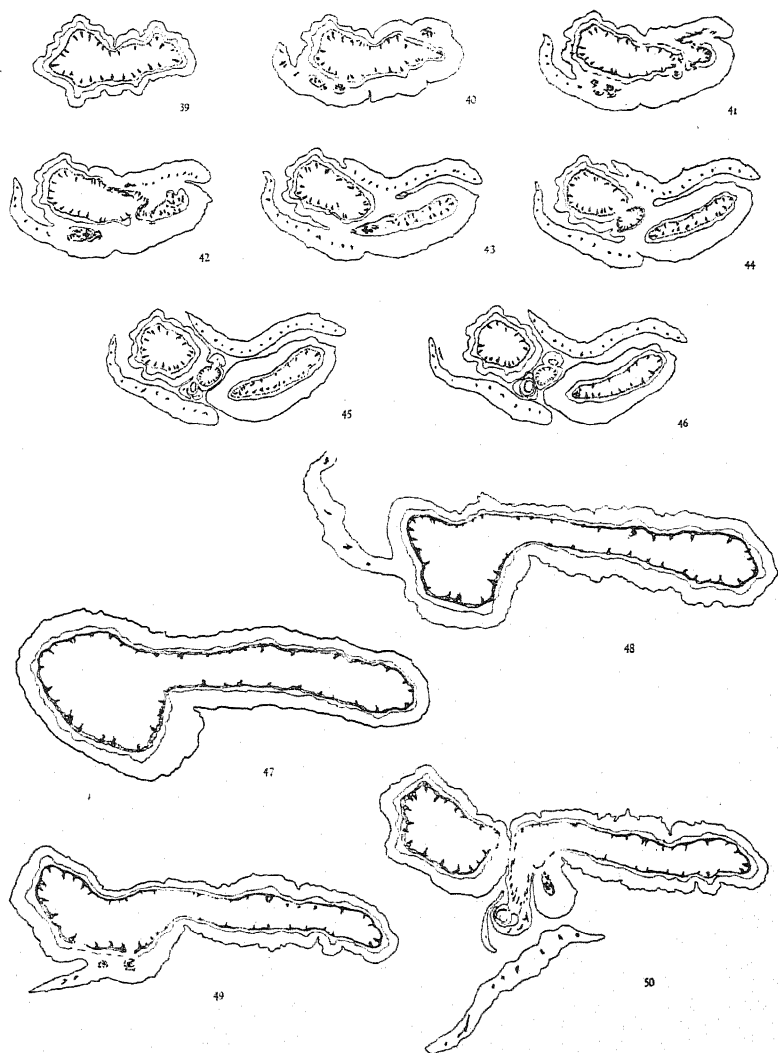
(3) In which a fasciated leaf is involved. Fasciation may disappear after the production of a fasciated leaf. One experimental plant showed three traces given off at the abaxial end, two from the flat side and one from the end of the stele. The three traces then converged as in the production of a pulvinus. Then many of the bundles of the original stele, located at the abaxial end near the traces were progressively included in the petiolar stele. As this was taking place, two traces from the adaxial end of the stem, on the flat side opposite the two abaxial traces, moved horizontally in the cortex to be included finally as the last bundles of the petiolar stele. The petiole was now greatly fasciated, being composed of three traces from the abaxial end, about twelve bundles of the original fasciated stem, and two traces from the adaxial end. When the fasciated petiole and its axillary bud diverged the stem above was cylindrical and composed of only 16 of the original 34 bundles.

The fasciated leaf did not have a definite pulvinus, but in the organization of its stele a convergence of bundles similar to that occurring in normal foliar development, occurred first at one end and later at the other end of the stele. At the abaxial end the pulvinar-like arrangement involved the three traces from that end, while at the opposite end the two adaxial traces were involved. The convergence of the traces was, however, of short duration, those at the abaxial end having separated even before the adaxial traces were included in the stele.

An almost identical case in another plant is illustrated in figures 39-46. Two traces on the upper right hand side of figure 40 left the stele and merged before the trace at the end departed. Simultaneously, the two adaxial traces at the lower left hand side appeared. Five ridges on the upper left hand sector of the figure can still be identified with five similar ridges of the contour of the fasciated stem before any changes occurred, as shown in figure 39. The rest of the outline has changed with the advent of foliar development, especially through enlargement of the cortex. The three traces at the abaxial end and many other bundles of the stem are now being arranged into the petiolar stele (figs. 41, 42), bundles from the upper side crossing through the pith to the lower side. The adaxial traces then complete the petiolar stele (fig. 43). When stipules, leaf, and axillary buds diverge the stem is normal (figs. 44, 45, 46).

In the last two cases described the stem returned to normal apparently by partitioning of the tissues of the fasciated stem between a large fasciated petiole, with its axillary buds, and a cylindrical stem. The latter is

similar to a sector of the original fasciated stem. The fasciated petiole, however, is much larger than the abaxial sector of the parent stem and differently shaped. Probably this is due to a combination of the elements



Figs. 39-46. The fasciated stem (39); abaxial and adaxial traces on opposite sides of stem. The contour is altered except at upper left (40); beginning of petiolar organization (41); incorporation of cauline bundles into stele (42); adaxial traces forming end of petiolar stele (43); axillary bud (44); separation of leaf and axillary bud (45, 46). The stem is now normal. The contour of the upper left hand sector is still similar to that of fig. 39.

formerly included in the abaxial sector plus additional tissue attending foliar development.

(4) In which another fasciated leaf is involved. In the examples of leaf-sectoring so far described, at least some of the bundles concerned in the make-up of the foliar vascular system were leaf traces. An important example was found, however, in which the leaf-sector was directly transformed from an abaxial sector of the fasciated stem into a petiole (figs. 47-55). There were two nodes close upon the place at which leaf-sectoring occurred. At the first node the leaf was represented only by two stipules with a subtended bud. After the divergence of the bud the shape of the adaxial sector was somewhat altered (fig. 48). Shortly above, a leaf developed from the side opposite the first leaf (lower side of figs. 49, 50). Beside it was a misplaced "axillary" bud. At this stage the opposite sides of the stele were converging (fig. 50) preparatory to the formation of two steles, much as in bifurcation. The physical separation of the two parts occurred almost immediately, with the petiole and "axillary bud" still attached to the abaxial branch (figs. 51, 52). Up to this point the phenomenon was like that of bifurcation in which the adaxial branch becomes normal. The fasciated branch, however, was determinate, bearing leaflets of typical mesophyll structure.

There was but a single outstanding exception to the recognition of this as a typical leaf and that was the development of a small bud lateral to the first leaflet (fig. 53). The rest of the structure was typically foliar (figs. 54, 55) terminating, however, in two leaflets.

From a comparison of vascular anatomy, three types of leaf-sectors may be distinguished: (1) that similar to the normal leaf in which the foliar stele enters the cauline stele through leaf traces; (2) that in which the stele of the leaf-sector is composed partly of traces and partly of the bundles of the parent stem which have not entered the cortex, (3) that in which the leaf-sector is identical with a sector of the fasciated stem.

#### DISCUSSION AND CONCLUSIONS

As has often been indicated, the dissolution of the fasciated condition is a process antithetical to its origin. In the latter, the change is from cylindrical to fasciated (of common occurrence in many plants, but rare in the scarlet runner bean), while in dissolution the change is from fasciated to cylindrical. In most of the cases noted in this study the shoot was fasciated at the base. Several plants were found, however, in which the branch originated as a cylindrical structure and became fasciated only later. Whether the fasciated shoot has originated from a single meristem, or from a fusion of several, cannot be decided without additional evidence.

In the cases where the shoot changes from normal to fasciated there can be no doubt that a single stem is involved in which but two alternative



Figs. 47-55. Fasciated stem (47); change of shape above first node (48); traces at second node (49); petiole and axillary bud of second node. Stem is constricting (50); separation of two branches, petiole and bud still attached to abaxial segment (51); separation of leaf and bud of second node (52); attachment of a leaflet; and the formation of a bud (53); other leaflets (54), two terminal leaflets (55). The stem above the leaf sector is normal.

processes may take place: the fusion of the apical meristem with its axillary buds, or an alteration in shape of the apical meristem through a change in the direction of cell division.

The bilateral outline of the cross-section of a fasciated stem does bear resemblance to the cross-section of a normal stem through an axillary bud. The tissues are continuous and the difference in size and maturity between the stem and bud is strikingly like that of a fasciated stem with adaxial and abaxial differentiation. This may be but a superficial similarity. On the other hand, very young buds were found, especially in the axil of trifoliate leaves, having fasciated axes and showing no indication of fusion. Furthermore, flattened apical meristems indicate that fasciation originates in a single structure.

The fasciated axillary shoots of *Phaseolus multiflorus* are in a state of unstable equilibrium which is manifest in the tendency to return to normal. The frequency with which natural fissures occur, and abnormal tropistic activity, indicate the establishment of uncoordinated centers of local growth. This is further manifest in the establishment of prominent ridges which give to fasciated shoots the superficial appearance of compoundness, and which have frequently been given as an argument for the fusion hypothesis origin of fasciation. Corrugation of the outline of the stem is characteristic of the normal plant; it is merely accentuated in the abnormal state. Georgescu (1927) believed that bifurcations arose from the formation of buds on the apical comb of the fasciated stem, which again is a process of establishment of local growth areas. That such regions possibly may arise by wounds in the apical meristem is suggested from Pilkington's (1929) studies. She artificially produced bifurcations in *Lupinus albus* by a median slit of the apex. In bifurcations observed in the study, however, there were no indications of injury.

Furthermore, normal foliar development results from the inception of a region of local growth with a subsequent development peculiar to leaves. Under certain unknown conditions such regions of special physiological activity may be initiated in a cellular mass which up to that point had developed, presumably under a set of different conditions, as a part of a stem, as in cases of leaf-sectoring.

Priestley (1929) especially emphasized the presence of areas of localized growth and differentiation in the shoot, which were definitely correlated with foliar development. So striking was sectorial growth that he considered the shoot as composed of independent units, and espoused Celakovský's "shoot-unit."

The data gleaned from the phenomena of bifurcation and leaf-sectoring fully confirm the existence of regions of local growth, although morpho-

logical significance of a phytonic nature should not be attached to it. Probably it is better to look upon these regions as physiological units of growth with vertical coordination. The shoot as a whole, in spite of its differential sectors, even when of indefinite shape, as in fasciations, is an organized whole with definite tissue relations. When the regions are considered in minutia there is a definite gradient from one sector to the next, from cell to cell. It is in this way that the shoot is radially coordinated, but over a very limited area. It is thus that most of the tissues are unaffected when a given mass of cells divides into two masses, as in a bifurcation or in certain sectors of the shoot during leaf-sectoring. The effect of bifurcation is very local, and that of leaf-sectoring, although of greater extent, never affects the whole organ. Extended vertical coordination, in contrast to limited radial effects, is probably a phase of the polarity shown by the shoot as a whole. The intergradation between structures of foliar and cauline nature in certain leaf-sectors emphasizes the difficulty of deciding where one begins and the other ends. The classical division of the shoot into leaf and stem is of practical value and should be retained on that basis. The term "leaf," however, should carry the implication of a specialized portion of the shoot, as a branch in direct continuity with the stem, together with which it forms a physiological unit of organization. While the homology between leaf and stem is not finally proven, the bulk of evidence points in that direction. The transformation of tissue sectors of cauline nature into leaves, which is of common occurrence in fasciated shoots of *Phaseolus multiflorus*, is here submitted as additional evidence in support of this view.

#### SUMMARY

1. Fasciated axillary shoots of *Phaseolus multiflorus* return to normal, or become less fasciated, by means of naturally occurring fissures, by bifurcation, and by leaf-sectoring.
2. A mature fasciated shoot may become almost cylindrical by the splitting off of a vertical sector, or by atrophy of a portion of the stem.
3. When fissures occur on young shoots the tissues which were in contact before the wound appeared are widely separated by the elongation of the rest of the stem.
4. Areas exposed by wounds heal by means of a cicatrix of dead cells, later followed by periderm formation. The break-up of the fasciated stem as mentioned in 2 and 3 above, is only of local significance.
5. Changes occurring in the meristematic regions as growth progresses bring about orderly reorganization of the fasciated shoot, resulting in a

less fasciated, or normal state. It expresses itself either as bifurcation or leaf-sectoring.

6. Prior to forking, the vascular system of the fasciated stem divides into two steles, later followed by the separation of the stem into two branches. The organization of the shoot is altered only in a very limited, furrowed region, above which the branches separate. The vascular differentiation and the contour of the branches are similar to what is characteristic of corresponding sectors of the fasciated parent shoot.

7. Dissolution of the fasciation often follows foliar development. In extreme cases a sector of the fasciated stem is bodily incorporated into a petiolar structure. The process is almost identical with bifurcation except that one of the branches is determinate and bears leaflets with normal mesophyll. In other cases, the leaf appears to be partly composed of a sector of the fasciated stem, although the bundles connecting the petiolar stele with that of the stem exists as leaf traces. Intermediate between these two types of leaf-sectors is one in which the petiolar stele is composed of leaf-traces at each end, and cauline bundles in between. There is also a type of reorganization in which the leaves appear as normal outgrowths from the stem. In these, the stem suddenly returns to normal above the node, as if the whole mass of cauline cells were shifted into a cylindrical form.

8. During the organization of a leaf-sector a large part of the shoot is affected. It is accompanied by additional lateral growth which alters the contour of sectors involved. The contour of the unaffected parts, however, can be identified with their corresponding sectors below, in the fasciated stem.

9. The existence of similar vascular differentiations and contours in corresponding sectors of the parent stem and its branches indicates a strong vertical coordination of the tissues of the shoot.

10. The data presented indicate that the shoot is an integral structure of which the leaves, the stem, and its ramifications are component parts, which act together as a physiological unit. Furthermore, specialized parts of the shoot, such as leaves, may influence the shape and construction of other parts with which they are in contact.

11. Branching is an inherent character of the shoot. In the normal plant it is manifest in the production of leaves and their axillary branches; in the abnormal plant, in addition to these, in bifurcation and leaf-sectors.

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## Notes on agarics from the western United States<sup>1</sup>

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(WITH PLATES 10 AND 11)

The species considered in this paper were collected by the writer (1936 b; 1937), in Washington, Oregon and California during the season of 1935. Certain common species are mentioned because of their occurrence in unusual habitats, but the majority are species which have either not been previously reported from North America or about the identity of which some ambiguity still exists. One new combination, *Omphalia delectabilis* (Pk.) Smith has been made. In all, nineteen species in nine genera are discussed.

Unless otherwise stated, the collection numbers and photographs are those of the writer. The collections have all been deposited in the Herbarium of the University of Michigan.

*COLLYBIA RACEMOSA* (Fr.) Quélet (Plate 11, fig. b). Pileus 3–10 mm. broad, obtusely conic, becoming plane or with a slight obtuse umbo, surface dry and opaque, innately silky, disk "fuscous,"<sup>2</sup> "drab" or paler toward the margin, margin usually curved in against the gills at first; flesh very thin, fragile, near drab in color, without a distinctive odor or taste; lamellae relatively broad, sharply and narrowly adnexed, close, "wood brown" to "avellaneous," edge even; stipe 4–6 cm.  $\times$  1 mm. equal above, tapering to a long "root" which terminates in a dull black more or less globular sclerotium, surface pruinose above, "hair brown" to "fuscous," lower portion covered with irregularly arranged short branch-like protuberances 2–3  $\times$  0.5 mm.; sclerotium watery grayish and homogeneous in section, with a thin dull black outer coat, 3–6 mm. diam.; spores 4–5  $\times$  2  $\mu$ , narrowly ellipsoid; basidia four-spored; cystidia not differentiated; pileus trama homogeneous, in tangential section the surface area appearing somewhat pseudoparenchymatous.

Closely gregarious near an old *Boletus*, Lake Tahkenitch, Ore., Nov. 11, 1935 (3416); near Marquette, Mich. during September, 1935, by E. B. Mains (35–31); and Lake Timagami, Ont. August 20, 1936, A. H. Smith and H. S. Jackson (4034). This very curious species apparently has not been reported previously from North America, and is apparently very rare in Europe. It resembles *Collybia tuberosa* (Fr.) Quélet in consistency and stature, but both the sclerotium and the peculiar branches on the stipe readily distinguish it.

<sup>1</sup> Papers from the Department of Botany and the Herbarium of the University of Michigan no. 617.

<sup>2</sup> All color names within quotation marks are taken from R. Ridgway, Color Standards and Nomenclature, Washington, D. C. 1912.

*HYGROPHORUS FRAGRANS* Murrill—Pileus 6–12 cm. broad, broadly convex then plane, in age the margin often elevated and the disk with or without a low obtuse umbo, viscid, disk “flesh ochre” to “flesh color,” margin whitish or tinged incarnate in age, opaque, remaining inrolled and white cottony until near maturity, in age the gluten often staining sordid ochraceous; flesh thick, pale incarnate near the surface, white near the stipe, odor faintly fragrant, taste mild; lamellae bluntly adnate, becoming subdecurrent in age, subdistant, 6–7 mm. broad, nearly equal or tapering slightly toward the edge, white or flushed pale incarnate, edge even; stipe 10–20 cm.  $\times$  1–2 cm. equal or attenuated toward the base, solid, white within, at times nearly ochraceous orange at the base, surface subviscid, more or less appressed fibrillose below, covered with conspicuous white scurfy points over the upper half, often beaded with drops of water, staining ochraceous to orange-ochraceous when handled, the stains becoming darker in age, spores  $7-9 \times 5-6\mu$ , broadly ellipsoid, yellowish in chloral hydrate-iodine solution; basidia four-spored; gill trama of divergent hyphae.

Gregarious under mixed hemlock and redwood, Trinidad, Calif., Dec. 1, (3685) and Oric, Calif., Dec. 6, 1935 (3858). Apparently this species has been known previously from only the type locality in Oregon. It is possible that two color forms exist. The above description of typical material is of collection #3858. The pilei of collection 3685 were yellow rather than flesh color. The colors were “warm buff” on buttons and “cartridge buff” to nearly white in older caps. The flesh near the pellicle, however, showed a decided tendency to turn incarnate when cut or bruised. The specimens had obviously developed slowly but were still firm and in good condition. These specimens may represent a characteristically yellow variety of *H. fragrans* but until more material can be collected and studied it seems best to regard them merely as a group of faded fruit-bodies.

*HYGROPHORUS PSITTACINUS* Fr. ex Schaeff.

Gregarious under dense stands of second growth redwood, Trinidad, Calif., Nov. 30, 1935 (3688) and at Joyce, Wash. on grassy ground. This is a cosmopolitan species growing under conifers as well as in grassy pastures throughout western United States. In the eastern and northern regions it is found either in mixed forests or in open grassy wood lots of oak and maple. It seldom occurs in abundance but one usually finds a few fruit-bodies in the course of a week's collecting.

*HYGROPHORUS PUSTULATUS* Fr. ex Pers.—Pileus 2–4.5 cm. broad, convex, at times papillate, margin inrolled and cottony at first and plane or arched in age, viscid, glutinous when wet, ashy with a darker brownish disk (near “buffy brown”), somewhat virgate with radiating fibrils, opaque; flesh soft

and white, rather thin, tapering slowly to the margin, odor and taste not distinctive; lamellae close to subdistant, bluntly adnate, becoming somewhat decurrent, narrow (4-5 mm.), pure white; stipe 6-9 cm.  $\times$  5-8 mm. equal or slightly enlarged below, solid or stuffed at the apex, lower portion subviscid to viscid from the remains of the thin universal veil, whitish, the apex dry and covered by dark gray punctate points; spores  $7-9 \times 4-5\mu$ , narrowly ellipsoid; basidia four-spored; gill-trama of divergent hyphae.

Closely gregarious in an unused trail under redwood and fir, Trinidad, Calif., Dec. 11, 1935. This species is readily distinguished by the conspicuously punctate apex of the stipe. Apparently it has not been reported previously from North America.

*HYGROPHORUS RECURVATUS* Peck (Plate 11, fig. c).—Pileus 1-2.5 cm. broad, convex or disk slightly depressed, with or without a papilla, surface lubricous to subviscid when wet, disk rugulose or smooth, at times translucent striatulate on the margin, margin either entire and wavy or subpubescent, cuticle often cracking circumferentially in age and at times lacerate, "clove brown" to "olive brown" or "buffy brown," margin becoming paler in age; flesh thin, dark olive brown, fragile, odor and taste not noticeable; lamellae distant, decurrent, broad, grayish white; stipe 2-4 cm.  $\times$  3-6 mm. tapering slightly downward, solid, grayish within, colored like the pileus or paler below, glabrous, moist, occasionally faintly longitudinally striate; spores  $7-9 \times 4-5\mu$ , ellipsoid, yellowish in chloral hydrate-iodine solution; basidia four-spored; gill trama interwoven; pileus trama homogeneous.

Singly to gregarious in open pasture land, Trinidad, Calif., Dec. 7, (3883) and Dec. 9, 1935 (3923). Peck described the stem as white or whitish and in this respect the California collections differ from Peck's species. This discrepancy, however, does not seem to me to be of taxonomic significance. The fruit bodies in my collections had been exposed to the intense sunlight of the open pasture, and as a result the colors were darker than usual. The darkening effect of intense sunlight has been observed on several species which are well known to the writer. Fruiting bodies of *Mycena citrinomarginata* Gillet found on mossy hummocks in open pastures are much darker than fruiting bodies which have developed under dense shade. Very dark fruiting bodies of *M. citrinomarginata* were found in the same pasture with the *Hygrophorus*. The same color difference has also been observed between collections of *Collybia palustris* (Pk.) Smith from exposed and shaded sphagnum in the same bog.

*HYGROPHORUS VARIICOLOR* Murrill

Gregarious under fir and pine, Olympic Hot Springs, Olympic Mts. Wash., Oct. 19, 1935 (3253). The pilei measured 3-6 cm. broad and were "russet" to "cinnamon brown" on the disk. The color faded toward the

margin which is agglutinated fibrillose. The stems in my collection measured 6–10 cm.  $\times$  9–14 mm., and were equal above a narrowed base. The apex of the stem is pruinose and watery drops are often present; the basal portion is only slightly viscid. The spores measure  $7-8 \times 4-5 \mu$ . The gill trama is of divergent hyphae, and the basidia are four-spored. The brown colors and nearly dry stipe with its pruinose apex are distinctive. *Hygrophorus discoideus* Fr. is closely related but its spores and stature are smaller.

*HYPHOLOMA VELUTINUM* (Fr.) Quél

Scattered on soil under redwoods, Prairie Creek State Park, Oric, Calif., Dec. 4 (3750), and Dec. 7, 1935 (3865). The spores of this collection measure only  $7-9 \times 4-4.5 \mu$ , but are typical in color, shape and markings. The young pilei were almost pure white at first due to a dense fibrillose covering. Old pilei were innately fibrillose squamulose and "snuff brown," "tawny olive" or "sepia" in color.

*LACTARIUS SANGUIFLUUS* Fr.—sensu Ricken

Scattered under Douglas fir, Boulder Creek, Olympic Hot Springs, Olympic Mts., Oct. 15 (3163), Lake Crescent, Wash., Oct. 22, (3284) and Oct. 23, 1935 (3306). There was no noticeable odor or taste at the time the specimens were collected but a faint sharp odor developed after the fruit-bodies were dried. The dark red latex, the change to green in spots or over all in age, and the orange-ochre pilei are distinctive. This species was fairly abundant in the Olympics during October.

*LEPIOTA GLISCHRA* Morg.

Singly under fir, Whiskey Creek, near Joyce, Wash., Sept. 23, 1935 (2563). The pilei measured 2–4 cm. broad, and varied from convex to slightly umbonate. The thick layer of gluten which covers the pileus and stipe is "burnt siena" in color. The flesh of the pileus is pure white and cottony to the touch. The latter characteristic immediately distinguishes it from the *Hygrophorae* to which it has a superficial likeness. The margin of the pileus may be appendiculate from adhering patches of the jelly-like universal veil. The annulus is evanescent.

*MARASMIUS CHORDALIS* Fries.—Pileus 1–2 cm. broad, broadly convex, the disk soon depressed, moist, at first white hoary from projecting cystidia, glabrous and dull in age, "buffy brown" on the disk, "dark olive buff" near the margin, fading to sordid olive gray in age; flesh thin, soft and pliant, whitish; lamellae moderately broad, adnate or with a slight tooth, subdistant, equal, edge even; stipe 6–10 cm.  $\times$  2–2.5 mm., equal, flexible and tough, white pruinose and beaded with drops of a hyaline fluid at the apex, dark brown (almost "bistre") below, with a dense scurfy covering, pseudorhiza well developed; spores  $9-11 \times 6-8 \mu$ , broadly fusiform, yellowish in chloral hydrate-

iodine solution; cystidia rare to numerous on sides and edges of gills,  $40-60 \times 10-20\mu$ , fusoid-ventricose with acute or subcapitate apices; basidia four-spored; pileus trama corticated by a layer of upright pyriform cells,  $30-50 \times 8-18\mu$ , many with elongated apices and thus resembling the pleurocystidia.

Gregarious on humus, Joyce, Wash., Sept. 22 (2553, by William Church), Oct. 11 (3102); Oct. 14 (3143), and Lake Crescent, Oct. 28, 1935 (3376). This species, apparently unreported for North America, was rather abundant near the second growth Douglas fir in the vicinity of Joyce, Wash. It seemed to favor grassy places along the edges of the denser growth, and was particularly abundant on sites of abandoned logging camps.

*MARASMIUS FUSCOPURPUREUS* Fr.—sensu Ricken.—Pileus 2.5–4 cm. broad, broadly convex, becoming plane or with a turned up wavy margin, occasionally umbonate, when moist “chocolate” or darker blackish purple-brown, fading to near “pecan brown” or “onion skin pink,” often sulcate on the margin; flesh rather thick, whitish, firm but pliant, odor none, taste mild; lamellae close to subdistant, rounded-sinuate, rather narrow, broadest at the base, tapering slightly toward the margin, “fawn color” to “buff pink” near the edges, almost “chocolate” at the base; stipe 7–10 cm.  $\times$  2–3 mm., equal or with the base and apex enlarged, base covered by dense vinaceous-brown hairs; spores  $7-9 \times 3-3.5\mu$ , ellipsoid, yellowish in chloral hydrate-iodine; cystidia not differentiated; basidia four-spored; pileus trama homogeneous, surface layer very compact.

Gregarious under fir, Joyce, Wash., Oct. 28, 1935 (3394). This species was abundant under second growth fir after a period of cold wet weather at the end of October. The species as described and illustrated by Bresadola (1929) is said to possess cystidia. The pigment granules as described by Kühner (1930) were abundant in the stipe and along the hyphae forming the compact upper region of the pileus trama. The fruit-bodies fade somewhat in drying and become “sorghum brown” to “vinaceous brown.” Ricken gives the spores as  $6-7\mu$  long. The writer's measurements were made from spore deposits. The spores of the dried specimens when re-studied measured  $6-8 \times 3-3.5\mu$ .

*OMPHALIA ABIEGNA* Berk. & Br. sensu Lange (1930)

Gregarious on sticks and debris, Lake Crescent, Wash., Oct. 9, 1935 (3054). The colors were at first “medal bronze” on the disk to “lemon chrome” near the margin. At maturity they were “sulphine yellow” with a darker disk and faded to “martius yellow” or “light chalcedony yellow.” The gills were “pyrite yellow” at first, at maturity “pinard yellow.” Spores from deposits measure  $7-9 \times 4-5\mu$ . The basidia are four-spored, and cystidia are not differentiated.



*OMPHALIA LUTEICOLOR* Murrill

Singly to gregarious on fir logs, Lake Crescent, Wash., Oct. 10 (3070); Oric, Calif., Dec. 7 (3862); Berry Mt. Trinity Range, Calif., Dec. 9, 1935 (3912). The colors are "bitter sweet orange" to "salmon orange" and fade to "ochraceous orange" or "ochraceous buff." Only the faded pilei in the above collections were truly yellow. Murrill's painting which is with the type at the New York Botanical Garden pictures an orange fungus. The margin of the pileus varies from glabrous to sparsely fibrillose and the edge is sometimes fringed with overhanging fibrils. The gills vary from "Caupucine orange" to "salmon buff" and the stem varies from "orange" to paler shades of yellowish orange. The spores measure  $7-9 \times 4-5\mu$  in the type and become faintly yellowish in chloral hydrate-iodine. Spores from deposits measure  $8-10 \times 4-5\mu$ . The pileus trama is homogeneous and cystidia are not differentiated.

*OMPHALIA MARGINELLA* (Pers.) Jossierand & Maire

Gregarious on a cedar stump, Lake Crescent, Wash., Oct. 16, 1935 (3176). Jossierand and Maire (1931) have given an excellent account of this species. *Omphalia rugosodisca* Peck, which is rather common in north-eastern North America, is similar to *O. marginella* in every respect except the marginate gills, and should be considered only a variety of it. This species and its variety are exactly comparable to *Mycena haematopoda* (Fr.) Quél. and its variety *marginata* Lange, except that the marginate form of the *Omphalia* was described first and is thus "typical" for the species.

*OMPHALIA BISPHAERIGERA* Lange

Gregarious under spruce, La Push, Wash., Oct. 25 (3334); Lake Tahkenitch, Ore., Nov. 19 (3544); Oric, Calif., Dec. 5, 1935 (3791). For an account of this species see Kühner (1930) and Smith (1936a). The fruit-bodies in collection no. 3544 were characterized by four-spored basidia and the spores measure  $6-8\mu$ . Their structure is the same as in the two-spored form.

*Omphalia delectabilis* (Pk.) comb. nov. (= *Agaricus* [*Mycena*] *delectabilis* Peck, Ann. Rep. N. Y. State Mus. 27: 93. 1875; *Mycena delectabilis* (Pk.) Saccardo, Sylloge Fungorum, 5: 262. 1887; *Prunulus delectabilis* (Pk.) Murrill, N. A. F. 9(5): 323. 1916. *Omphalia nitrosa* Kauffman, Papers Mich. Acad. of Sci. Arts and Letters, 11: 202-203. 1930).

The spores of Peck's type at the New York State Museum, Albany, N. Y., measure  $7-8 \times 3-4\mu$ , the basidia are four-spored, and fusoid-ventricose cystidia measuring  $27-35 \times 7-11\mu$  are scattered on the sides and edges of the gills. Peck described the gills as close, not crowded, and his

figures are convincing. The western collections are identical with material collected in Nova Scotia in 1931 by Smith and Wehmeyer (1936). The gills of mature caps are usually subdistant to distant, but in small or immature individuals they often appear close. Because of the truly decurrent gills and the straight pileus margin of young fruiting bodies, this species belongs in the genus *Omphalia* in the section *Mycenariae*. It is very closely related to *Omphalia gracilis* Quél. Gregarious under second growth fir, Joyce, Wash., Oct. 2, 1935 (2784).

*PHOLIOTA AUREA* (Fries) Gillet (Plate 10)

This apparently rare but strikingly distinct agaric has been well described by Maire (1911), Ricken (1915), p. 459, and Overholts (1927). Overholts cites it as known in North America only from British Columbia. The writer found it growing gregariously in grass along the side of a road, Lake Crescent, Wash., Oct. 9 (3050) and Oct. 15 (3117), and in a similar location near the Elwha River Ranger Station, Oct. 25, 1935 (3355). The pilei in these collections measured 10–25 cm. broad, and the stems 8–20 × 2–5 (7) cm. The colors of the pileus and stipe varied from “raw sienna” to near “ochraceous tawny.” The granulose covering of the pileus and stipe is at first composed of pyramidal scales which soon become worn and as a result the entire surface is merely powdery. The lamellae are “light buff” to “warm buff” at first and “ochraceous buff,” or darker at maturity. As is shown in the photograph, the margin is conspicuously appendiculate at first. The spores in mass were “pale ochraceous buff” but appeared smooth and nearly hyaline under the microscope when fresh. Spores from dried specimens, however, are a golden brown under the microscope. Maire (1911) has pointed out that *Lepiota pyreneae* Quél is identical with this species.

*PSATHYRA TORPENS* var. *LEUCOPHAEA* Fr. Icones Hymen, Pl. 38, fig. 1.—Pileus 1–2.5 cm. broad, obtusely conic to oval at first, becoming broadly conic, convex or plane in age, surface glabrous and moist, hygrophanous, at first “cinnamon buff” on the disk and whitish toward the margin, striatulate, soon livid from the maturing spores, when faded grayish white and opaque, margin becoming crenate to scalloped at times; flesh membranous, very fragile, odor and taste not distinctive; lamellae close, narrow, adnate, white at first or pale grayish, soon purplish brown from the spores; stipe 6–12 cm. × 1.5–2 mm. pure watery white, very fragile, equal, hollow, somewhat pruinose near the apex, smooth below; spores 12–14 × 6–7 $\mu$ , ellipsoid, dark reddish brown under the microscope, purple brown in mass; basidia four-spored; cystidia on sides and edges of gills, 60–70 × 10–15 $\mu$ , fusoid ventricose, smooth; pileus trama corticated by a layer of upright pyriform pedicellate cells.

On humus and debris in woods and open grassy places under trees, Lake Crescent, Wash., Sept. 20 (2523) (2524). The palisade of pyriform

cells covering the pileus is similar to that found in the genus *Conocybe*. Kauffman in his notes gives the colors as "light vinaceous fawn" or "light vinaceous drab" and fading to "pale vinaceous fawn." Judging from both Kauffman's and my own observations, this is one of the common species in the Olympics. In addition to the typical fertile material a sterile form was found in considerable abundance (coll. 2524). The colors were similar to those of the fertile caps at first but in age became dull white or faintly ochraceous. Fries' (1877) illustration is very representative of my collections. The spores of the Washington material agree best with the measurements given by Bertrand (1901).

*STROPHARIA SEMIGLOBOIDES* Murrill (Plate 11, fig. a).—Pileus 2–4.5 cm. broad, obtusely conic, becoming convex to plane, glabrous, glutinous, "honey yellow" to "olive ochre" at first, becoming "reed yellow" to "primrose yellow" in age, faintly striatulate, margin without adhering fibrils or fibrillose patches; flesh rather thick on the disk (3–4 mm.), tapering gradually or abruptly part way to margin, dull sordid olive ochre, taste mild; odor not distinctive; lamellae moderately broad, equal, close, adnate, soon seceding, at first white, soon "drab," edge even; stipe 8–11 cm.  $\times$  3–4.5 mm., with a long vermiform pseudorhiza 4–10 cm.  $\times$  2–3 mm. equal above, tubular, flesh "citron yellow" to "barium yellow," surface sheathed to near the apex by a glutinous sheath terminating in an evanescent annulus which is floccose above and glutinous below, apex yellow and pruinose, lower portion appearing whitish or pallid due to a layer of white fibrils beneath the gluten; spores 8–10  $\times$  4–5  $\mu$ , ellipsoid, dull purple brown under the microscope, dark purplish brown in mass; cystidia on the gill edge only, scarcely differentiated, 36–40  $\times$  8–10  $\mu$ , clavate, smooth, slightly longer than the basidia; basidia four-spored; pileus trama with a thick gelatinous pellicle, beneath it a poorly defined region of inflated cells, the remainder floccose.

Singly on humus under spruce, Lake Tahkenitch, Ore., Nov. 18, 1935 (3524). The type consists of a single small fruit-body the microscopic characters of which are exactly as given above.

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#### Explanation of plates

Plate 10, *Pholiota aurea* (Fr.) Gillet.  $\times$ 2/3.



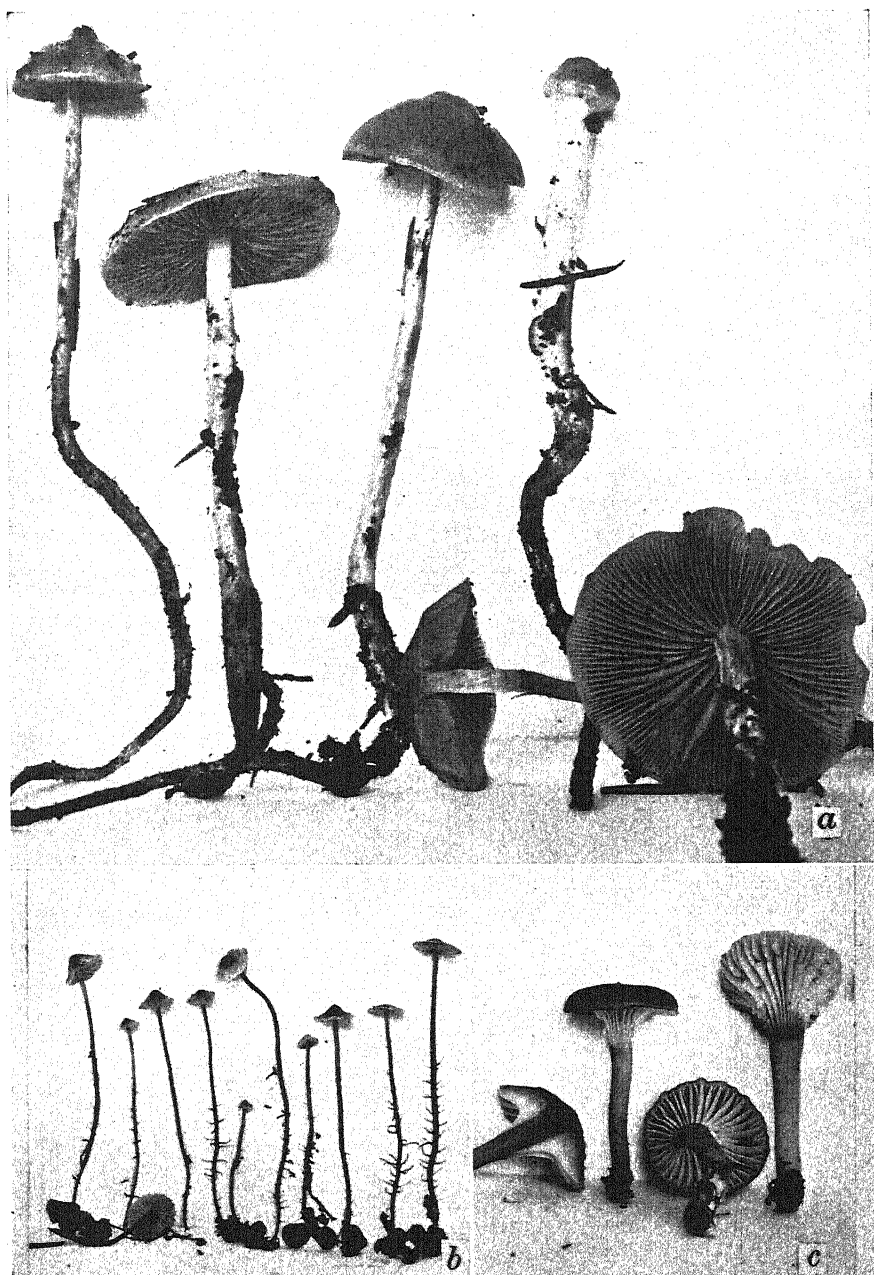
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Plate 11, fig. a, *Stropharia semigloboides* Murrill.  $\times 1$ .

Plate 11, fig. b, *Collybia racemosa* (Fr.) Quelet.  $\times 1$ .

Plate 11, fig. c, *Hygrophorus recurvatus* Peck.  $\times 1$ .



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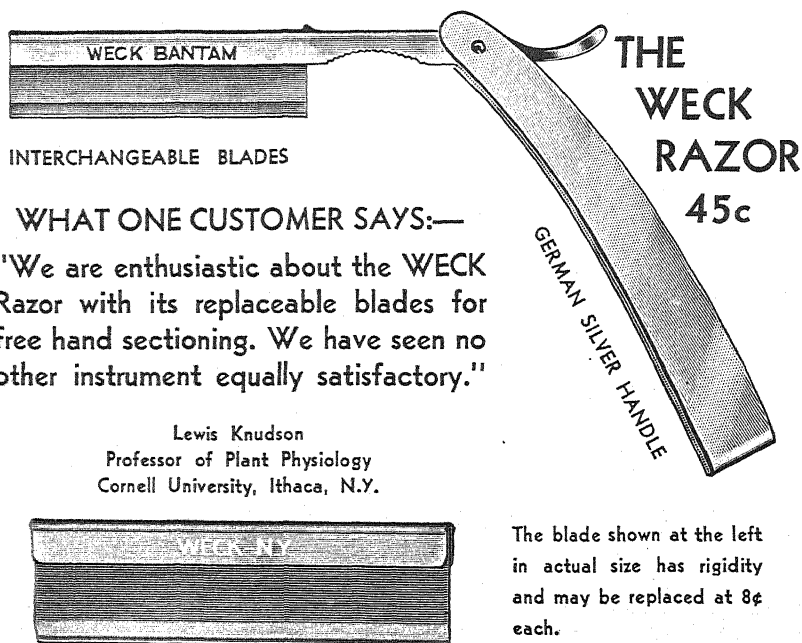
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## Hybridization experiments with natural variants of *Hypomyces Ipomoeae*

A. W. DIMOCK

(WITH ONE FIGURE)

Mycological and phytopathological literature contain numerous reports of variants of fungi which have been isolated directly from nature or have appeared in pure laboratory cultures. Although evidence is proffered which leaves little doubt that many of these differ genetically from the normal or parent strains, only a few reports have come to the writer's attention in which genetic differences have been proved experimentally by hybridization. Dodge, (1930, 1931) and Wülker (1935) have thus proved the character "albinistic" (conidia-free) in *Neurospora sitophila* to be determined by a factor allelomorphic with "normal" (conidial). The evidence presented by Dodge (1930) suggests that this character may have been carried by some of the nuclei in a heterocaryotic strain (Arl. 10) at the time of its isolation from nature, rather than having arisen as a mutant in the vegetative mycelium of subsequent laboratory cultures. Zickler (1934) has shown that certain sectorial variants appearing in the vegetative mycelium of laboratory cultures of *Bombardia lunata* were initiated by genic mutation. Both Dodge and Zickler have also studied variants of the classes "induced variants" and "ascospore variants" defined below. Lindegren (1933, 1934) has likewise made detailed investigations of ascospore variants in *Neurospora*.

The term "natural variants" is used to designate variant strains isolated directly from nature or appearing as sectors or dissociants in supposedly pure gametophytic laboratory cultures of the normal or parent strains. The term is used in contradistinction to the terms "induced variants" and "ascospore variants," the former denoting variants arising as the results of specific treatment with chemicals, heat, X-rays, etc., the latter indicating variant types developing as the primary growth from individual ascospores isolated from either inbred or hybrid asci. It is understood that these are merely terms of convenience and are applied only to variants whose abnormalities are intrinsic rather than transient effects of differences in culture media. Hybridization experiments with two natural variant strains of *Hypomyces Ipomoeae* have been carried out by the writer during the past year, and though the investigations were limited in extent, a brief report seems desirable at this time.

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## HISTORY AND DESCRIPTION OF THE NORMAL AND VARIANT STRAINS

a) *Normal*. The "normal" tester-strains of *Hypomyces Ipomoeae*, 3-3 bearing sexual reaction factor *A*, and 3-14 bearing sexual reaction factor *a*, will be referred to throughout this paper as the *normal* type. The history of these strains has been given in detail in a previous paper (Dimock, 1937). Briefly, both strains originated from single ascospores isolated from a perithecium developing on an elderberry stem which had been inoculated with mycelium from a naturally infected sweet-potato root. On nearly all media, plantings of the *normal* strains developed fluffy white cultures at the centers of which conspicuous macrospore masses were formed. The mycelium and the macrospore masses in some cases became slightly pigmented, but no pigment was diffused into any of the media on which the strain was cultivated. Cultures of the *normal* type on malt-extract and potato-dextrose agar media are illustrated in figure 1.

b) *Diffusa*. At the time of isolation of the single-ascospores yielding the *normal* tester-strains, 13 single ascospores were also isolated from a second perithecium on the same elderberry stem. Four of these single-ascospores developed cultures of the *normal* type, and 6 developed cultures which were indistinguishable from one another but which differed from the *normal* in the several respects noted below. One of the cultures of this latter sort (2-7), which proved to bear sexual-reaction factor *A*, was taken as the type of the *diffusa* strain. Of the three remaining single-ascospores isolated, one developed a culture of *normal* appearance, but of considerably slower growth rate; another developed a culture of *diffusa* appearance, but of growth rate similar to the preceding; and the third developed an extremely slow-growing culture of the *diffusa* type. These three cultures were not studied further.

The *diffusa* strain differs from the *normal* in the possession of a slightly slower growth rate and a more diffuse type of marginal growth, due possibly to a different mode of hyphal branching. When grown on malt-extract agar, this strain develops reddish pigment in the aerial hyphae of the central portion of the cultures, but the substratum does not become pigmented. On potato-dextrose agar, however, both aerial mycelium and substratum become intensely pigmented, as is clearly shown in figure 1. Perithecial fundaments are formed in all pure cultures of *diffusa* regardless of the sexual-reaction factor carried. It is believed that the *diffusa* strain was carried over in the original isolation from nature, and that the perithecium from which the type was isolated was a *normal* × *diffusa* hybrid. The arguments favoring this opinion will not be presented

here since they depend on as yet unpublished observations, and clarification of the point is not of vital importance to this paper.

c) *Rosa*. This strain originated as a rose-colored sector in a monoconidium culture of the *normal* tester-strain 3-14 (*a*) on malt-extract agar. The culture was removed from the original monoascospore culture of 3-14 by six consecutive monoconidial culture generations, and the variant sector had its inception at a point 15 mm. out from the monoconidium planting. Mass transfers of mycelium from the sector yielded cultures which were obviously mixtures of *normal* and rose-colored hyphae. Of 25 conidia isolated from the margin of this sector, 19 produced pure *normal* cultures and 6 produced pure rose-colored cultures. One of the latter, designated as R, was taken as the type of the *rosa* variant.

Cultures of the *rosa* strain on malt-extract agar differ from those of the *normal* and *diffusa* strains by the presence of a strong rose-colored pigmentation of both mycelium and medium. When grown on potato-dextrose agar, an intense purplish pigmentation of mycelium and substratum, somewhat resembling that of the *diffusa* strain, is produced (fig. 1). No perithecial fundaments have been observed in any culture of the *rosa* variant, whether of one sexual-reaction or the other.

Although the above variant strains were believed to be pure and homocaryotic, several consecutive monoconidium culture-series of each were studied in the manner described by Hansen and Smith (1932) in order to make doubly certain of this before commencement of hybridization experiments. All individuals in each culture-series of both strains were true to type and exhibited a high degree of uniformity of cultural characters.

#### HYBRIDIZATION STUDIES

a) *Normal*  $\times$  *diffusa*. The constancy of the *diffusa* strain throughout numerous monoconidium culture-series and mass transfers strongly suggested it to be genetically different from the *normal* strain. Conclusive information concerning the nature of the difference, however, could be obtained only by analyses of the ascospore progeny of various matings of the strains involved. Extensive studies were not undertaken, but the data obtained leave little doubt that genetic differences were involved.

Nineteen single ascospores were isolated from an individual perithecium developing in a *normal* (3-14, *a*)  $\times$  *diffusa* (2-7, *A*) mating on a sterilized bean pod. Eleven of these single ascospores developed cultures indistinguishable from the *normal* type, and the remaining 8 yielded cultures indistinguishable from the *diffusa* type. No intermediate types appeared. In back-crosses with the two parent strains, 12 of the  $f_1$  cul-

tures were found to bear sexual-reaction factor *A* and 7 the factor *a*. The 11 to 8 distribution of morphologic type suggests that it is determined by a single allelomorph factor pair, or by pairs of closely linked factors which behave as a unit. The factor or factor-group determining expression of the *diffusa* characters will be designated by *D*, its allelomorph, which determines expression of the normal characters, by *d*. As regards sexual-reaction and morphologic character, the genotypes of the *normal* and *diffusa* parents in the above cross may then be written *ad* and *AD*, respectively and the 19 *f*<sub>1</sub> cultures segregated into the four possible groups as follows:

<i>Ad</i>	<i>ad</i>	<i>AD</i>	<i>aD</i>
5	6	7	1

The single *aD* *f*<sub>1</sub> culture was back-crossed with the *diffusa* parent, 2-7 (*AD*), and was mated with *normal* tester-strain 3-3 (*AD*). Although primary perithecia appeared at about the same time in both cases, the inbred perithecia in the *diffusa* × *diffusa* mating were few in number and no secondary perithecia were formed, whereas both primary and secondary perithecia were produced in great numbers in the *normal* × *diffusa* mating. All of the inbred (*diffusa* × *diffusa*) perithecia examined were found to lack ostiola and had hence failed to discharge their ascospores, which no doubt accounted for the non-appearance of secondary perithecia in this mating. *Diffusa* × *normal* perithecia, as well as *normal* × *normal* inbred perithecia, were always ostiolate and exuded ascospores in abundance. Secondary perithecia were produced in considerable numbers about such primary perithecia. The question might well be raised as to whether the perithecia assumed to have been produced secondarily were truly secondary in nature or merely further primary perithecia. While experiments specifically designed to determine this point were not carried out, the following observations support the assumption. First, the writer has previously shown (1937) that *normal* conidia of either sexual reaction may "spermatize" perithecial fundaments of opposite sexual reaction. Second, microscopical examination had revealed that perithecial fundaments in all stages of development are present in the hyphae immediately surrounding primary perithecia in matings in which the *normal* strain is one of the parents. Third, microscopical examination has further revealed that many ascospores in the masses exuded from perithecia of which one of the parents is *normal* germinate *in situ*, indeed, some germinate within the perithecial cavity and send their germ tubes out through the ostiolum. It is reasonable to assume that these ascospores may, like conidia, function

in the "spermatization" of perithecial fundamentals. Finally, in matings between *normal* and *aborta* strains of *H. Ipomoeae* which will be reported elsewhere, perithecia bearing only *normal* ascospores in typical 8-spored asci were formed about the primary, hybrid perithecia whose asci are regularly 4-spored. The regular appearance of these normal inbred perithecia in *normal* × *aborta* matings could be satisfactorily explained only by the assumption that the *normal* ascospores which were discharged from the hybrid perithecia functioned in the "spermatization" of perithecial fundamentals which developed in the hyphae of the *normal* parent. It is not suggested that all perithecia which develop subsequent to the formation of the first primary perithecia in fertile matings are secondary in nature. New primary perithecia continue to appear for an indefinite period.

Forty-one single ascospores were isolated from one of the *diffusa* inbred perithecia and planted on malt-extract agar slopes. Of these, 38 developed cultures indistinguishable from one another and from parallel monoconidium cultures of the original *diffusa* strain. The other three developed cultures which, unlike the *diffusa* type, produced a strong reddish pigmentation of the malt-extract agar substratum and showed marked restriction of growth. The variation here was not in the direction of the *normal* strain, but farther away from it. The nature of this variation was not investigated, nor was the distribution of the sexual-reaction factor pair, *A/a*, determined for this population.

The above data, while limited in extent, are strong evidence that the chief cultural differences between *diffusa* and *normal* are determined by a single pair of allelomorphic genes, *D/d*, which segregate independent of the sexual-reaction genes, *A/a*. This of course implies the presence of at least two linkage groups in *Hypomyces Ipomoeae*. The possibility that the morphologic characters may be determined by two or more genes is not excluded, but if such is the case, they are so closely linked that they behave as a unit.

b) *Normal* × *rosa*. The type culture of the *rosa* variant was assumed to bear sexual reaction factor *a* inasmuch as it originated as a sector variant in a culture of the *normal* tester-strain (3-14) bearing that factor. The assumption was verified by the appearance of fertile perithecia in matings with *normal* tester-strain 3-3 (*A*), while matings with tester-strain 3-14 (*a*) remained sterile. The hybrid perithecia which developed in the former matings were of normal appearance and bore 8-spored asci. Single ascospore plantings on malt-extract agar slopes were made with spores obtained from the ascospore masses being exuded from each of two

hybrid perithecia, 23 from one and 41 from the other. Of the 64 cultures which developed, 27 were of the *normal* and 37 of the *rosa* type, no intermediates appearing. This suggests that, as in the case of the *diffusa* variant, the expression of cultural characters differentiating the *rosa* and *normal* strains is determined by a single allelomorphic gene pair or by closely linked pairs which behave as a unit. The *rosa* gene or gene-group will be designated by *R*, and its *normal* allelomorph by *r*.

Ten of the  $f_1$  cultures, three *normal* and seven *rosa*, were taken at random and mated with both *normal* tester strains. Two of the *normal* and six of the *rosa* proved to bear sexual-reaction factor *a*, one of each the factor *A*. The sexual-reaction factor borne by each of the remaining *normal*  $f_1$  cultures was determined by "spermatization" with microconidia of one of the *normal* tester-strains in the manner described in an earlier paper (Dimock, 1937). Spermatization tests in which *normal* microconidia were added to check cultures of the *rosa* parent showed this method to be unreliable for determination of the sexual-reaction factor groups of *rosa* cultures. Unfortunately, it was not possible in the time available to mate the remaining  $f_1$  *rosa* cultures with the *normal* tester strains. The distribution of the  $f_1$  cultures among the four possible genotypes, as far as determined, is indicated below:

<i>normal</i> (total 27)		<i>rosa</i> (total 37; 7 tested)	
<i>ra</i>	<i>rA</i>	<i>Ra</i>	<i>RA</i>
17	10	6	1

Attempts were made to inbreed the *rosa* variant, but in no case were perithecia formed in *rosa*×*rosa* matings. It will be recalled that in the description of the variant it was noted that perithecial fundaments were never observed in pure cultures, whether of one sexual-reaction or the other. These phenomena, together with the fact that mycelial matings of compatible *rosa* and *normal* strains were always fertile, suggest that *rosa* strains of both sexual-reaction groups may be completely male in nature. Such a suggestion, however, should not be accepted without further supporting evidence.

No *rosa*×*diffusa* matings were made. It is therefore not known whether *rosa* and *diffusa* genes for morphologic character are multiple allelomorphs of a single *normal* gene, nor whether they lie in the same or in different linkage groups.

It seems appropriate here to make a few observations as to the ability of the two variant types to persist in competition with the *normal*. *Diffusa* and *normal* strains of the same sexual-reaction might be expected to persist

together indefinitely, for conidium formation seems to be about as prolific in one as in the other, and the growth rate of the *diffusa* strain is but little lower than that of the *normal*. Ascospore formation could of course play no part in such an association. If, however, a *diffusa* strain were placed in competition with a *normal* strain of *opposite sexual reaction*, the latter would increase at the expense of the former, in time possibly replacing it altogether. The reason for this is that *normal* mycelia of both sexual reactions would become established soon after discharge of spores from the first hybrid perithecia, and, being highly fertile, would soon form inbred perithecia in abundance which would liberate only *normal* ascospores, thus permitting a rapid build-up of that strain. *Diffusa* mycelia of both sexual reactions would of course become established as quickly as those of the *normal*, but in this case the effect of inbreeding would be negligible since inbred *diffusa* perithecia are produced only sparsely, and those produced are, in culture at least, non-ostiolate and thus incapable of normal spore liberation. The actual rate at which the *normal* might be expected to supplant the *diffusa* strain would be rather difficult to determine, since ascospores are more of theoretical than practical importance in the perpetuation and spread of this fungus.

The fate of the *rosa* strain would be even more unfortunate than that of the *diffusa* strain, for conidium formation here is much less abundant than in the *normal* strain. Hence, even when competing only with a *normal* strain of the same sexual reaction, the *rosa* strain would probably be rapidly replaced. In competition with a *normal* strain of opposite sexual reaction, the *rosa* strain would not have even the slight benefit of inbreeding which might be claimed for the *diffusa* strain. Either of these variants, however, when removed from competition with the *normal* might well persist indefinitely. These examples provide concrete evidence as to why the "normal" strains of some fungi maintain themselves so well in nature rather than being supplanted by the numerous variants which must be continually arising.

#### SUMMARY

Two variant strains of *Hypomyces Ipomoeae* which are classed as "natural variants" are described and illustrated. One of these, *diffusa*, is believed to have had its origin in nature. The other, *rosa*, appeared as a sector variant in a monoconidium culture of the *normal* strain on a malt-extract agar slope.

Both variants have retained their distinguishing cultural characters in numerous single-conidium and mass-transfer cultures, showing no tendency toward reversion or further variation.



Hybridization experiments have strongly indicated that each of the variants differs from the *normal* in a single gene or in a few closely linked genes. In both cases the gene or gene-group determining expression of the variant characters lies in a different linkage group from the sexual-reaction gene. Whether the *diffusa* and *rosa* genes are in the same or in different linkage groups has not been determined.

The *diffusa* variant produced a few fertile, non-ostiolate perithecia when inbred, but attempts to inbreed the *rosa* variant were unsuccessful.

Neither of the variant strains is well adapted to persist in competition with the *normal*.

The writer is deeply indebted to Prof. H. N. Hansen for advice and criticism during the course of the investigation and the preparation of the manuscript.

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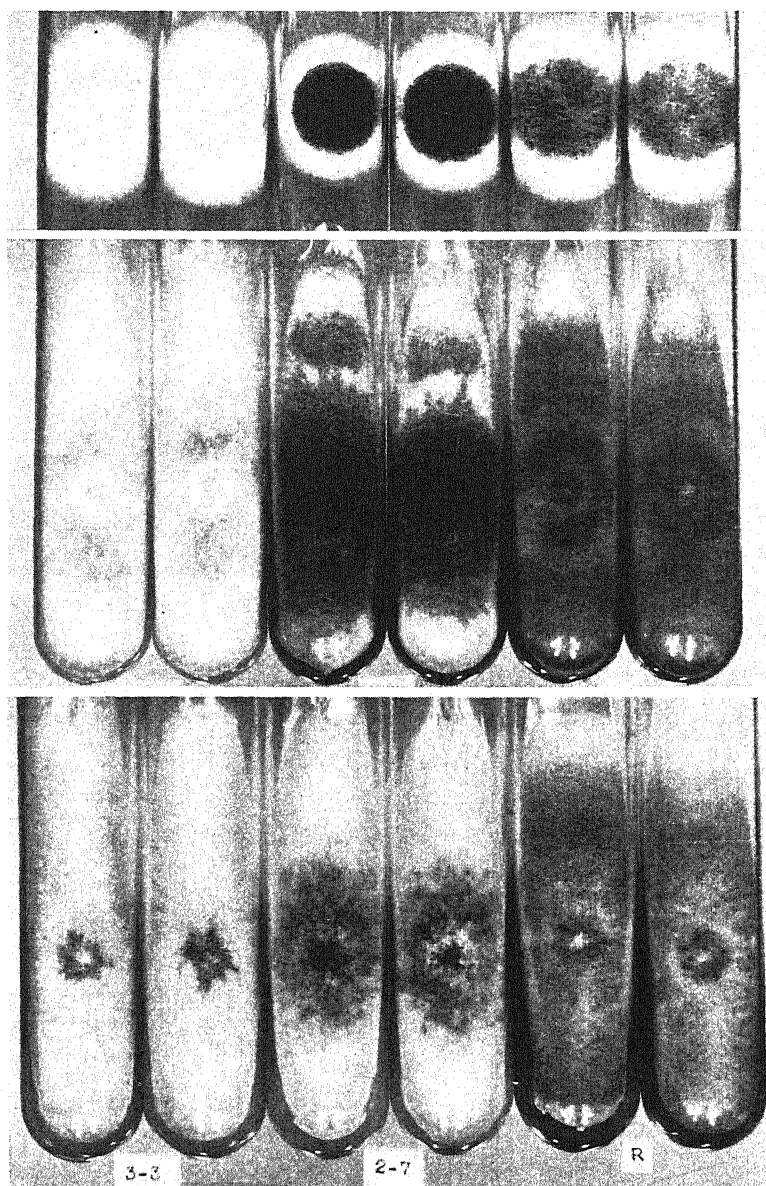


Fig. 1. Left to right: 2 $\frac{1}{2}$  monoconidium cultures each of *normal* (A), of *diffusa* (A), and of *rosa* (a). Top row, 3-day-old cultures on potato-dextrose agar; middle row, same cultures 9 days old; low row, 9-day-old cultures on malt-extract agar.



## Annotations upon the California flora—I

JOSEPH EWAN

(WITH TWO FIGURES)

In the preparation of a botanical survey of the San Gabriel Mountains of southern California, problems have arisen as to the correct application of binomials of certain species within the area, involving in many instances species of wider range. Some realignments of these species confused in the literature are presented here.

Pertinent collections have been studied in the herbaria of Pomona College, Los Angeles County Museum, Stanford University, California Academy of Sciences and the University of California. The author is grateful to the curators of these collections for their genial courtesy. I am indebted to Dr. Carl Epling, Dr. Theodor Just, Dr. P. A. Munz and Mr. C. A. Weatherby for the communication of critical memoranda upon types, along with numerous and varied favors. Especially to Dr. W. L. Jepson, whose viewpoints, botanical library and collections have been freely shared, do I express my thanks. It is a pleasure to acknowledge the assistance in photography given by Mr. W. C. Matthews and Mr. Everett Dempster of the University of California.

### 1. *ALLIUM PARISHII* WATS.

*Allium Parishii* Wats., Proc. Am. Acad. **17**: 380. 1882, based on *Parish Bros.* 1344 from mountains near Cushenbury Springs, north slope of San Bernardino Mts., V. 1882. ("Cushenberry" acc. Parish's original label and his writings but "Cushenbury" on the San Gorgonio Quad., U.S.G.S. The "Cushenberg" of Jones, Contr. W. Bot. **10**: 20. 1902, is a misprint.) Photograph of type, in Gray Herb., studied. Isotype at Dudley Herb. is a poor match for the type specimen.

*Allium Parishii* has been confused with *Allium monticola* Davidson (*A. Peirsonii* Jeps.). They are not synonymous but geminate species, one occupying the San Bernardino Mountain area and *monticola*, the adjoining San Gabriel Range. They may be distinguished as follows:

#### ALLIUM PARISHII

*Scape* comparatively slender, usually erect, bearing an umbel of 6-12 flowers.

*Tepals* linear-subulate their entire length, ca. 3 mm. wide, not noticeably outwardly spreading.

*Filaments* ribbon-like, lower half exactly wing-dilated passing gradually into thread-like upper portion.

#### ALLIUM MONTICOLA

*Scape* stout, often curving, bearing an umbel of 10-16 (or 26) flowers.

*Tepals* evenly acuminate from base (ca. 3-4.5 mm. wide) to the subulate tip, often strongly flaring.

*Filaments* slender, lower portion oblong along insertion, abruptly contracted to a uniformly filamentous upper portion.

*Ovary-crests* narrowly triangular, acute, without a median fold, irregularly few-toothed.

*Habitat* alkaline spots in the pinyon (*Pinus monophylla*) belt, rarely on talus.<sup>1</sup>

*Ovary-crests* usually slender, with a median lengthwise fold, erose, coarsely several-toothed.

*Habitat* granitic gravels of rock slides in Yellow Pine (*Pinus ponderosa*) and White Fir (*Abies concolor*) belts or on higher bald summits; intolerant of alkaline soils.

Coming as it does from a botanical blind-spot, *Allium Parishii* is little known in the field and rare in herbaria. Apart from the explorations of Parish along the north slope of the San Bernardino Mountains in the years 1882, 1885, and 1886, the area has been only sporadically visited, and then chiefly the vicinity of Cushenbury Springs. Before Parish, in May 1876, Dr. Edward Palmer collected in the "Mohave River District" or about the headwaters of the Mohave River on the north slope. What now appear to be puzzling species in the Bear Valley region of the San Bernardino Mountains may be better understood when this area lying between the arid Transition Zone and the floor of the Mohave Desert is thoroughly explored.

## 2. *ALLIUM MONTICOLA* DAVIDSON.

*Allium monticola* Davidson, Bull. S. Calif. Acad. Sci. 20: 51 (photograph on p. 50), "August" 1921. Received at Mo. Bot. Gard. Library 31 VIII 1921 *vide* Nell C. Horner. Based on *Robert Kessler* (No. 1924 as Davidson's accession no.) from Mt. Markham, San Gabriel Mts., VI 1921. Type (now) in L. A. Museum Herb. studied.

*Allium Peirsonii* Jepson, Fl. Calif. 1: 274. 24X1921, based on *F. W. Peirson* 3 from Baldy (Mt. San Antonio), east trail, 9400 ft., 8 VII 1918. Type in Jepson Herbarium studied.

*Allium Parishii* [Wats. misapplied by] Davidson, Bull. S. Calif. Acad. Sci. 15: 33. 1916, as to *Burlew* coll.; by Jepson, Fl. Calif. 1: 273. 1921, as to synonym; in part by Abrams, Ill. Fl. Pac. States 1: 389. 1923, where fig. 951 adequately illustrates *A. monticola*, not *A. Parishii*; by Munz, Man. S. Calif. Bot. 87. 1935, as to plants of San Gabriel Mts. Not Watson (1882).

*Allium Brewerii* [Wats. misapplied by] Jones ex Johnston, Pl. World 22: 83. 1922, as to San Gabriel Mts. colls. Jones retracted this determination in Contr. W. Bot. 15: 55. 1929. Topotype material of *A. Brewerii* Wats. has been examined in fresh condition, by the kindness of Dr. Mary L. Bowerman, and the distinctness of the two species is clear. The flowers pass through a color range in the fresh material at hand from "deep rose color" (Watson) to pale pink. Two isotypes of *A. Brewerii* Wats. studied.

<sup>1</sup> *Munz & Hitchcock* 12,784 from Crystal Creek, 6500 ft., is labelled as growing in "talus."

*Allium monticola* is an endemic species of the dry coarse gravels of steeply inclined talus slopes or rock slides (sliding shingle) of the San Gabriel Mountains. It has been most often confused with *A. Parishii* Wats. (*q. v. ante*). There are, however, characters of habit, dilation of the filaments, ovary crests and floral bracts that distinguish the two species. Whereas Watson described *Parishii* as having the "stigma somewhat lobed," *monticola* generally has no stigmatic lobing whatever. Phrases descriptive of the lobing of stigma are at best but relative and commonly unavailing in keys unless the user has an adequate series of sheets before him for comparison. In this sense, *Allium Parishii* may be said to have the stigma lobed to an intermediate degree between *fimbriatum* and *monticola*.

*Representative colls. of Allium monticola*: San Gabriel Mts.: Pine Ridge, w. of Mt. Pacifico, 5500 ft., *Ewan* 7399 (bulbs quite palatable); Lowe-Markham divide, 5350 ft., 10 VI 1918 *Peirson* 1; Mt. Islip trail above Big Cienega, 6800 ft., *Ewan* 2695; Rock Creek (head of), 6500 ft., *Peirson* 267; San Antonio Peak, 9000-9800 ft., *Hall* 1235; Baldy (San Antonio Pk.) summit, 10,000 ft., 22 VIII 1917 *Johnston*; Telegraph Peak, 9000 ft., *Johnston* 1543; San Antonio Canyon (head of), 8000 ft., *Johnston* 1446; Icehouse Canyon, 6500-7000 ft., *Peirson* 5355; North Baldy, 3 VII 1908 *Abrams & McGregor*.

Jones has called attention to the propagation of this species by means of "filiform underground runners" which may "vary from a millimeter in length to four inches" (*Contr. W. Bot.* 15: 55. 1929). This observation deserves notice in the field, particularly with reference to the related *Allium Parishii*. Possible seed differences are yet to be determined. In *Allium monticola* I find but one seed commonly develops.

### 3. QUERCUS DUMOSA VAR. ELEGANTULA (GREENE) JEPSON.

*Quercus Macdonaldi* Greene var. *elegantula* Greene, West. Am. Oaks 26. 1889, based on a specimen collected by *Greene* "late in March" [probably 27th,] 1885 at Temecula Canyon, (then "San Diego Co."), Riverside Co., Calif. Type not located.

There is a sheet in Calif. Acad. Sci. Herb. (no. 1029) bearing a label in *Greene's* hand as follows: "*Q. dumosa* × *Q. oblongifolia*? 12-15 ft. high. Temecula Cañon, Mar. 27." From this date and from *Greene's* statement in the original description to the effect that authentic material is to be found at the California Academy of Sciences, this sheet would be nominally selected as the type. Indeed, Katherine Brandegee has indicated "Type" on the sheet in question, though *Greene* himself did not do so. But there are several points, which critically bear upon the selection of the "type," regarding this collection standing at variance with the original

description. Thus the leaves in this collection are not "lance-oblong in outline, coarsely and sharply toothed or lobed from base to apex" but ovate-oblong, sparingly and irregularly serrate to subentire, plane, subglabrous or finely puberulent. Unfortunately this collection is in flower with the leaves quite immature. In characters of inflorescence, especially the capillary nature of the pedicels and stalks, the specimen strongly resembles *Quercus agrifolia*. Since this collection fails to match the original description it seems ill advised to consider it the "type." A subsequent statement of Greene (West Am. Oaks pt. 2, pl. 29. 1890) that "as collected by me at first, late in March, the twigs bore only young leaves not full-grown" further places this collection. A collection recently acquired by the University of California Herbarium through the incorporation of the Lemmon Herbarium may, however, be designated as the lectotype. This collection (U.C. Herb. 338415) represents the later "journey of [June] 1889" and is of full-grown foliage (fig. 1), probably safely considered to be a mature specimen of the earlier flowering collection discussed above. Greene apparently followed up this oak on his return trip of 1889 with veritable zeal for there is at Notre Dame University in his own herbarium a series of eight sheets (nos. 37389-37396) of this expedition of 1889, illustrating the several variations discussed by Greene on p. 63 (opposite pl. 29) of his West American Oaks. This collection (U.C. Herb. 338415) satisfactorily follows the original description and is therefore designated as the lectotype.<sup>2</sup>

Parish's collection of this oak made at Temecula on 5 November 1891 as represented in the University of California Herbarium is most heterogeneous. His collection comprised sixteen numbers, at least, and was reported upon in Zoe (4: 346. 1894). Except for *Parish 2276* which is indubitable *Quercus agrifolia*, they apparently represent fluctuating colonies of *Quercus dumosa* with probable admixtures of *Engelmanni*. Their true position can only be told after detailed field work in the region, carried on over several seasons with marked trees in the manner of studies in *Salix*. The name *Quercus dumosa* Nutt. var. *elegantula* (Greene) Jepson, published in Jepson, Man. Fl. Pls. California 274. 1923, here taken up as expressive of its probable affinity, does not include the reference to "Monrovia" given by Jepson, which is the next species discussed in this paper.

#### 4. *Quercus grandidentata* sp. nov.

*Quercus dumosa* Nutt. var. *elegantula* Jepson, Man. 274. 1923, in part, as to "Monrovia," actually based on *Geo. B. Grant 1091* from that locality.

<sup>2</sup> Lectotype = "type" chosen when unquestioned "type" lost.



Fig. 1. *Quercus dumosa* var. *elegantula* (Greene) Jeps. Temecula Canyon, Riverside Co., Calif., June 1889, *E. L. Greene*, coll. (Lectotype in Univ. Calif. Herb.)



Not *Q. Macdonaldi* var. *elegantula* Greene (1889). *Quercus dumosa* [Nutt. as amplified by] Trelease, Mem. Nat. Acad. Sci. 20: pl. 203a 1924, as to *Geo. B. Grant 1091*, designated as "representing one of the most lobed forms of the polymorphic species *Q. dumosa*."

Arbor parva circiter 6 m. altitudine coma compacta rotundata ramulis inferioribus subpendulis; ramulis junioribus subfuscis et dense tomentellis demum glabris cineries; foliis habitus Myricae lineari-oblongis, 5-8 cm. longis, praesertim supra medium remote grandidentatis rarius subsinuatis, dentibus paucis deltoideis 3-5 mm. altis salientibus mucronatis, pagina superiore glabra nitida inferiore cinereo-tomentosa interdum senectute pilis carptim deciduis; cupulis poculiformibus diametro 18 mm. longitudine 12 mm. in basi raro tomentellis, squamis tuberculatis; glandibus oblongis 18-21 mm. longis incrassatis obtusis longitudinaliter lineatis nitentibus.

Type: Monrovia, 2 miles above A.T. & S.F. RR. tracks, at mouth of Sawpit Canyon (Monrovia Canyon), Los Angeles Co., Calif., 750 ft., 27 XII 1934 *Ewan 8487* (acorns from type tree, 29 XI 1929 *Berry Campbell*). Univ. Calif. Herb. 533189. Tree about 20 ft. tall among chaparral of piedmont mesa.

In addition to the type collection (isotype set to be distributed) the following collections have been studied: same loc., type tree, 2 III 1929, *Ewan 302*; *ibid.*, 27 XII 1934, *Ewan 8487a* (small leaf form, the blades aver. 4 cm. long, 1 cm. wide); *ibid.*, *Ewan 8487b* (large leaf form, the blades to 9 cm. long); *ibid.*, *Ewan 8487c* (rounded-sinuate-lobed leaf form, the blade distinctly obovate or obcuneate); Monrovia, *Geo. B. Grant 1091* (as seen in several herbaria very uniform); Thompson Creek Wash 3 mi. n.e. La Verne, 1325 ft., clay knoll, *Louis C. Wheeler 252* (tree ca. 10 m. tall).

Distinctive for its Myrica-like leaves, *Quercus grandidentata* is little known in the field and the available collections are few. Associated with such ligneous species as *Quercus agrifolia*, *Rhus diversiloba*, *Salvia apiana*, *Senecio Douglasii* and *Lepidospartum squamatum*, this oak grows in deep gravel-alluvium borne across the piedmont mesa from the canyons of the San Gabriel Mountains above. It is to be looked for all along this piedmont mesa of the San Gabriel Valley. As far as can be determined now, the first collection of the oak was made by George B. Grant at "Monrovia" on 14 June (*Grant 1091*) distributed with printed label as "*Q. McDonaldii* Greene," an insular species best developed on Santa Catalina and excellently represented by *Hall 8276* from Hay Press Spring. Grant's exact station for *grandidentata* at Monrovia is not known but the author discovered a tree at the mouth of Sawpit Canyon (Monrovia Canyon) on 2nd March 1929 (*Ewan 302*). The tree was not fruiting on this date. Berry

Campbell, who accompanied the author on the March trip, collected a very few acorns from the same individual on 29th November 1929. These acorns have been placed with the type sheet. F. W. Peirson relates that he believes a tree on New York Avenue in Altadena was this species, but it was destroyed. No collection was made.

*Quercus grandidentata* may bear the same relationship to *Engelmanni* as *Quercus rydbergiana* of New Mexico bears to *undulata*. *Quercus rydbergiana* Cockerell (the type of which is illustrated as pl. 155, Mem. Nat. Acad. Sci. 5: 20) is a very local element known from the vicinity of Las Vegas Hot Springs, 7000 ft., and is marked by singularly "sinuately sub-lobed" leaf dentition. Perhaps these two oaks, *grandidentata* and *rydbergiana*, are recent derivatives from *Q. undulata* and *Q. Engelmanni* respectively; both wide-ranging species in the regions where found. Sargent (Silva N. Am. 8: 5. 1895) suggests a probable natural hybrid origin for such oaks. He writes: "the rarity of these trees, which are always found growing with individuals of the species from which they are supposed to be derived, the variations in the leaves on one tree and often on one branch, and their apparent inability to spread in the forest, support the theory of their hybrid origin." With *Quercus grandidentata* the likely parent species would be *Q. dumosa* and *Q. Engelmanni* but the sorting of characters is not apparent.

To orient *Quercus grandidentata*, *Q. Engelmanni*, *Macdonaldi* and *dumosa* var. *elegantula*, the first two species for their suggestive relationship and the third for the historic association of *grandidentata* with that misunderstood oak of the Temecula region, the characters are outlined as follows:

##### 5. *Eriogonum minus* (Johnston) comb. n.

*Eriogonum umbellatum* Torr. var. *minus* Johnston, Bull. S. Calif. Acad. Sci. 17: 64. 1918, based on *Johnston 1692* from summit of Mt. San Antonio, 10,000 ft., "common in rocky ground," 22 VIII 1917. Type (U.C. Herb. 205968) and isotypes examined.

Sub-alpine dwarf; stems woody, glabrescent, shortly and repeatedly branching to form a loose caespitose mat upon a deep-seated taproot; flowering stems borne on the terminal shoots, 2 to 9 cm. high, densely strigose-tomentose; herbage white-lanate, the felt tardily deciduous; leaves in a congested tuft, the blades suborbicular, barely acute, 5 to 8 mm. long, abruptly contracted to a short petiole, the petiole somewhat dilated and indistinctly channeled, scarcely if at all bifacial, strigose-hairy; umbels simple, with a circlet of foliaceous bracts at the summit of the peduncle, the rays 2 to 4, short (4 to 8 or rarely 16 mm. long); involucre saucer-shaped, the lobes ovate,

TABLE 1  
Comparison of selected characters of four species of *Quercus*

QUERCUS GRANDIDENTATA	QUERCUS ENGELMANNI	QUERCUS MACDONALDI	QUERCUS DUMOSA VAR. ELEGANTULA
<p><i>Leaf-blades</i> narrow oblong (narrower than the other 3 species contrasted here), 5 to 8 cm. long, rounded at the base and entire for <math>\frac{1}{2}</math> to <math>\frac{3}{4}</math> length of the blade, then sinuate and finally regularly and uniformly coarsely dentate above, the teeth 5 to 9, spinulose-tipped, directed forward.</p> <p><i>Pubescent</i> of lower leaf surface a soft felt-like tomentum, this tardily deciduous, at no time as dense as in young <i>Q. engelmanni</i> but more persistent.</p> <p><i>Twigs of the year</i> strongly tomentose distally, thinly so below, gray and glabrate on old wood.</p> <p><i>Acorn cup</i> shallow, bowl-shaped, 18 mm. diam., 12 mm. deep, warty tuberculate and thinly tomentose about summit, the marginal scales comparatively small, glabrate.</p> <p><i>Nut</i> short-oblong, 18 to 21 mm. long, finely lineate and lustrous shining, distinctly truncate at summit, sparingly hairy about the prominent mucro (2 to 2.5 mm. long).</p> <p><i>Based on type, Tewan 8-487 and Monrovia, Geo. B. Grant 1091.</i></p>	<p><i>Leaf-blades</i> elliptic-oblong, entire, 4 to 6 cm. long, obtuse at apex, not at all sharp pointed, never spinose-toothed (young leaves subsinuate-serrate above, entire or nearly so below, narrowing uniformly).</p> <p><i>Pubescent</i> of lower leaf surface a tomentum of irregularly branched hairs when young, readily removable to give a glabrous shining surface with venose-reticulate markings. This tomentum persists about leaf-bases, irregularly deciduous in patches elsewhere.</p> <p><i>Twigs of the year</i> densely tomentose distally, scantily tomentulose below, gray and glabrescent on old wood.</p> <p><i>Acorn cup</i> shallow, bowl-shaped, 16 mm. diam., 9 to 10 mm. deep, corrugate with low papillae, strongly fulvous-tomentose about summit, the marginal scales minute and indistinct, glabrescent.</p> <p><i>Nut</i> ovate-oblong, 20 to 28 mm. long, finely grooved or scored as well as lineate, dull shining, narrowed to summit, conspicuously hairy about the mucro (1.5 mm. long).</p> <p><i>Based on Pasadena, Geo. B. Grant 1086; Liveoak Canyon, La Verne, 1 XI 1931, H. A. Wheeler; Baldwin Estate, San Marino, 9 XI 1932, Ep-ling.</i></p>	<p><i>Leaf-blades</i> oblong-ovate, acute or obtuse at base, 5 to 7 cm. long, regularly and uniformly coarsely dentate, the teeth 7 to 11, directed forward, often with secondary tooth toward the acute mucronulate tip.</p> <p><i>Pubescent</i> of lower leaf surface a thin tomentum, soft felt-like when young, early evenly deciduous and glabrescent, leaving patches of persistent tomentum.</p> <p><i>Twigs of the year</i> densely tomentose over whole length, shaggy pubescent, glabrescent on old wood.</p> <p><i>Acorn cup</i> rather deeply hemispherical, conspicuously tuberculate (Greene).</p> <p><i>Nut</i> ovate-oblong, acutish, less than an inch long (Greene).</p> <p><i>Based on orig. desc. and plate 34; also Santa Catalina Isl., Hall 8276 and Pelican Bay, Santa Cruz Isl., Abrams &amp; Wiggins 69.</i></p>	<p><i>Leaf-blades</i> narrowly oblong or ovate, 5 to 7 cm. long, obtuse or cordate at base, variously irregularly margined, with or without a mucronate apical tooth or a few spinose teeth on one or both sides of blade toward apex.</p> <p><i>Pubescent</i> of lower leaf surface a thin tomentum, especially on young leaves, as scattered stellate hairs not as a close indument.</p> <p><i>Twigs of the year</i> glabrate or slightly hairy about nodes, shining red-brown distally, less so on old wood.</p> <p><i>Acorn</i> not known.</p> <p><i>Based on lectotype discussed elsewhere in this paper, Temecula Canyon, Greene VI 1889, U.C. Herb. 338412.</i></p>



Fig. 2. (a) *Eriogonum stellatum* Benth. Swartout Valley, San Gabriel Mts., Ewan 8358. (b) *Eriogonum minus* (Johnston) Ewan. Summit North Baldy, San Gabriel Mts., Ewan 8353.

hairy within, erect or spreading, not prominently reflexed; calyx deep rich red, 4 to 6 mm. long, glabrous, narrowed to a distinct stipe-like base, the segments obovate, rounded, with a central black blotch.

The author has discussed elsewhere<sup>3</sup> the "probationary method in systematic botany" as applicable to two ferns, *Pellaea mucronata* (D.C. Eaton) D. C. Eaton and its geminate species, *Pellaea compacta* Maxon. Again a species of wide distribution, *Eriogonum stellatum* Benth., borders closely upon an endemic derivative species, *Eriogonum minus*. Here, as in the *Pellaea* relation, the phylogeny is better shown by treating the two elements as distinct species.

The accompanying photograph (fig. 2) of the two species *Eriogonum stellatum* and *E. minus* from material collected in the San Gabriel Mountains illustrates the differentia existing between them. Fig. 2a, is *Eriogonum stellatum* Benth. taken at Swartout Valley, 6500 ft., Ewan 8358 and fig. 2b, *E. minus*, summit of North Baldy (Now needlessly renamed Mt. Baden-Powell), 9000 ft., Ewan 8353. *Eriogonum stellatum* Benth. is a common plant on the desert (north) slope of the San Gabriel Range and also occurs in similar montane habitats to the north and south of that area. The striking sulphur yellow flowers have imposed the vernacular name "Sulphur Flower." It is a resident of the *Artemisia tridentata* flats at the lower edge of the Yellow Pine belt. The plant of montane southern California is *E. stellatum* Benth. and not *E. umbellatum* Torr. as commonly accredited by authors. This determination was made at Royal Botanic Gardens, Kew, by Dr. W. L. Jepson from a study of the critical authentic collections represented there. The two species are, furthermore, separate and distinguishable, *E. stellatum* ranging in general to the south of *E. umbellatum* and characteristic of the more arid interior regions of western North America.

*Eriogonum minus* characterizes a coterie of mountain summit habitats, far above the Yellow Pine belt, of the San Gabriel, San Bernardino and San Jacinto Mountains. On these summits it comprises both a constant and distinctive colonial population. In fact, *Eriogonum Kennedyi* var. *austromontanum*, *Oreonana vestita* and the less frequent endemic *Monardella cinerea*, make a well-marked formation, the members of which exhibit the same low, more or less cushion-like growth-form. Typical collections of *E. minus* are: San Gabriel Mts.: Mt. Williamson summit, 8200 ft., Ewan 8309; Mt. Islip summit, 8200 ft., mats in pure gravel, Fosberg & Ewan 4884; Mt. Hawkins, 12 VII 1930, Sweet, West & Crow; North Baldy, 9000 ft., Ewan 8353, same loc., Abrams & McGregor 609; Mt. San

<sup>3</sup> Jour. Wash. Acad. Sci. 25: 363-370. 1935.

Antonio, 10,000 ft., *Abrams* 1930, same loc., *Peirson* 21, same loc., 9930 ft., VIII 1914, *Gordon Surr.* San Bernardino Mts.: Mt. San Gorgonio, 25 VIII 1905, *Charlotte Wilder.* San Jacinto Mts.: [Probably summit San Jacinto Peak,] VIII 1915, *A. J. Perkins.*

Stations altitudinally below that of *E. minus* and above the normal range of *E. stellatum* exhibit plants morphologically intermediate. These intermediates may possibly represent established hybrids having originated at a time, long past, when the two species occupied the same territory. I do not believe such intermediate plants, always occurring as individuals rather than as colonies and of variable morphological characters from specimen to specimen, invalidate the recognition of *Eriogonum minus* as a species. Were these intermediates more numerous relative to the whole population of the two species in the region, one would have sound reasons for questioning the advisability of maintaining them apart as species. But from my field experience in southern California they appear to be nowhere frequent or even to comprise small colonies but occur as random individuals at elevations midway between the mass of population of each species. These intermediates commonly show bicolored reddish and yellow flowers, the colors being freely mixed over the umbel. It will be remembered that typical *E. stellatum* is sulphur yellow at anthesis, reddening on passing into ripe seed. The intermediates show a mixed color not only in seed, but in anthesis as well. *Eriogonum minus*, on the other hand, is permanently deep rose red at all stages. The colors shown by these species and their intermediates may have genetic significance.

Intermediate collections seen are as follows: Mt. San Antonio trail, *Abrams* 1940 (rays of umbel 12–14 mm. long), Cucamonga Peak, 8500 ft., frequent on stony north slope, *Munz* 6099 (rays of umbel 10 or even 28 mm. long); Mt. San Antonio, 9000 ft., *Abrams* 2681.

6. *Garrya flavescens* Wats. var. *pallida* (Eastw.) Bacigalupi comb. n. *Garrya pallida* Eastw., Proc. Calif. Acad. Sci. ser. 3, 2:287 "issued June 3, 1902," based on specimen collected by *Eastwood*, VII 1899, in the Kings River Canyon, near Fresno-Tulare Co. line, southern Sierra Nevada. Note on itinerary given by *Eastwood* (l.c. 285). Type (Calif. Acad. Sci. Herb. 31548) studied. Also described almost simultaneously (issued 7 days later) by *Eastwood* in *Flora of South Fork of Kings River* (Sierra Club Publ. 27:50) which was "ready for circulation about June 10th." (cf. *Sierra Club Bull.* 4:153. 1902).

Dr. Rimo Bacigalupi has indicated in his "Systematic study of the genus *Garrya*" (Stanford Univ. M.A. thesis XII 1924, ined.) what I believe is the relationship between the Great Basin *Garrya flavescens* Wats.

and the shrub usually known under that name of the southern Sierra Nevada and montane southern California. The leaves of the type material show a pubescence of straight "fine silky" hairs, thin as not to obscure the underlying venation, heterochromous, the youngest shoots plumbeous-gray, while the older shoots are glabrescent and yellowish; the bracts of the catkins are remarkable, being sericeous or "silvery, silky canescent from the densely appressed hairs." *Garrya pallida* was said when described by Eastwood to be "nearest to *G. Fremontii* Torrey" but its closest affinity is to *flavescens*, as indicated by Munz (Man. S. Calif. Bot. 362. 1935) and by Jepson (Fl. Calif. 2 : 676. 1936).

The following collections of var. *pallida* from the San Gabriel Mountains have been examined: Rock Creek, 4750 ft., *Pierson 138*, same loc. 4500 ft., *Abrams & McGregor 568*; Strawberry Ridge, 5000 ft., 23 VI 1910, *F. Grinnell Jr.*; Millards Canyon (head of), trail from Alpine Tavern to Switzers, 4000 ft., *Ewan 2057*; San Antonio Canyon, 5750 ft., *Johnston 1578* (cited by Johnston, Pl. World 22 : 111. 1919, as *G. Veatchii* var. *Palmeri*, which group is also present in the range); Table Mt., Swartout Valley, 7000 ft., *Ewan 9880*.

Leaf size varies widely among shrubs of the same colony. One shrub on Table Mt. had nearly exclusively small leaves, smaller than the half-dozen other shrubs of the hillside colony. These small leaves were crowded at ends of the branches to give a false idea of compactness to the shrub as a whole. Its congeners had an open, more loosely branching habit with their leaves standing at right angles to the stem, in the manner of species of *Arctostaphylos*.

7. *Hugelia densifolia* Benth. subsp. *austramontana* (Craig) comb. n. *Gilia densifolia* (Benth.) Benth. var. *austramontana* Craig, Bull. Torrey Club 61 : 391. 1934, based on *Munz 8341* from Nellie, Palomar Mts., San Diego Co. Type in Pomona Coll. Herb.

*Hugelia pluriflora* (Hel.) comb. n.

*Gilia pluriflora* Heller, Muhlenbergia 2 : 113. 1906, resting on *Gilia virgata* var. *floribunda* Gray, Proc. Am. Acad. 8 : 272. 1870, which in turn rests on a coll. made by [Rev. A.] Fitch, perhaps in the vicinity of Sacramento where he is known to have botanized. Further synonyms given by Craig (l.c. 414). Heller did not intend that his "Sunset, Kern Co., Calif." collection should be construed as the type of his *G. pluriflora*, a renaming necessary under the homonym rule, but was itemizing, with annotations, the collections of the "season of 1905."

Craig has reviewed (l.c. 385) the shifting position of the segregate

genera of *Gilia* and "because of the lack of absolute characters to separate the groups" merges the genus *Hugelia* with the then unnatural genus *Gilia* (*sens latissimus*). Though it is admittedly difficult, if not perhaps impossible, to settle upon mutually exclusive generic characters in this polemoniaceous complex, phylogeny is best served by maintaining compact more ideally natural genera to express our uncertain ideas as to natural relationships rather than by combining several somewhat overlapping species-groups, such as *Navarretia*, *Langloisia* and *Linanthus*, into the then segmented unnatural genus *Gilia*.

8. *Monardella viridis* Jeps. subsp. *saxicola* (Johnston) comb. n.

*Monardella saxicola* Johnston, Bull. S. Calif. Acad. Sci. 18 : 19. 1919, resting on Johnston 2133 from near Browns Flats, San Gabriel Mts. Isotype in Univ. Calif. Herb. studied.

*Monardella hypoleuca* var. *saxicola* (Johnston) Jepson, Man. Fl. Pls. Calif. 882. 1925.

Both *Monardella viridis* (type, in Jepson Herb., examined) and subsp. *saxicola* have been studied in the field by the author. At the head of the Wolfskill Fork of San Dimas Canyon, San Gabriel Mts., subsp. *saxicola* is associated with *Pseudotsuga macrocarpa* and *Quercus chrysolepis* on partially shaded gravelly benches. Above Adams Springs, in the North Coast Range of Lake Co., *Monardella viridis* is found on well-drained gravelly slopes beneath *Pseudotsuga taxifolia*, *Pinus ponderosa* and *Quercus Kelloggii*.

Although accorded species rank by Epling (Ann. Mo. Bot. Gard. 12 : 55. 1925), *Monardella saxicola* cannot be maintained as a species distinct from *M. viridis*. Collections made in the last decade, especially those of Louis C. Wheeler, have considerably extended our knowledge of *M. saxicola* and have shown the leaf characters used to separate this species from *M. viridis* of the North Coast Ranges to be valueless. However, most of the minor differentia enumerated by Epling hold good for a series of specimens. In addition, they may be distinguished as follows:

Calyx-lobes comose with long spreading hairs, the head of fruiting calyces conspicuously canescent from above.....	<i>M. viridis</i> .
Calyx-lobes short-pilose with short stiffish hairs, the head of fruiting calyces not conspicuously canescent from above.....	<i>M. viridis</i> subsp. <i>saxicola</i> .

The origin of such forms in nature, geographically widely separated and morphologically closely related, presents a significant problem in the genetics of the California flora.

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## On the classification of *Euphorbia* II. How should the cyathium be interpreted?

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In an earlier number of this journal (Croizat, 1936) the writer has wondered why the orthodox botanists who maintain *Euphorbia*<sup>1</sup> appear to have as weak a taxonomic case as the unorthodox taxonomists who so far have carved the genus. The cyathium, in particular, has been suggested to be inadequate for the definition of the genus, and of its segregates.

Mentioning "orthodox" and "unorthodox" authorities the writer is aware of accepting, for brevity's sake, adjectives that are current today, but ultimately will stand only as the remainders of a peculiar moment in the history of botanic thought. Systematic and floristic investigation has reached a point where it can be shown that, tested on performance, "orthodoxy" and "unorthodoxy" have less than shadowy existence. Bower (1928), Hall & Clements (1923), O. Schwarz (1936), Perrier de la Bathie (1932) using fundamentally identical or analogous methods of investigation come to diverse results in nomenclature. Hence the number of genera and species admitted in a work of classification is not a just criterion of value. Lumping, as the word goes, in no wise is sooner to be commended than splitting, for the primary issue of classification is one of concepts, not of names.

Understood as an issue of names the addition of *Diplocyathium* (Pax, 1931) to the canon of the "orthodox" genera of *Euphorbieae* is irrelevant, because it increases the burden of nomenclature of the Euphorbiaceae by about one-third of one per cent. Appraised as an issue of concepts this same addition is vitally important because it makes it possible to break up *Euphorbia* into very many monotypic or oligotypic genera with results ultimately fatal to concepts and to names alike. Precisely stated for the benefit of the practical taxonomist, the question of *Diplocyathium* is that of the limits within which certain constant anatomic characters (e.g., a double cyathium-structure) justify, or not, the announcing of genera that may be segregated from *Euphorbia*.

To answer this question it is essential to determine a scale of values that apply to *all* the characters whereby the species of the genus differ among themselves. The conceptual, i.e., taxonomic, issue is hopelessly beclouded if certain segregates are rejected *a priori*, as they are by the majority of modern botanists, on the ground that such genera are based upon habit-characters. If the issue is to be understood it is necessary to

<sup>1</sup> Except where otherwise noted, *Euphorbia* and *genus* mean the Linnaean genus. The generic and specific names accepted in this article are those agreeable to Boissier (1862), and/or Pax & Hoffmann (1931).

find out, among the rest, whether these habit-characters are the result of mere accident of environment as, for instance, is the prostrate habit of conifers in wind-swept regions, or of fundamental, hereditary alterations such as the prostrate habit of *E. sect. Anisophyllum* in which the main stem aborts with far reaching effect upon the axial type.

The cyathium is, however, the first structure that is offered for investigation, if for no other reason because it happens to be the organ upon which taxonomy has so far insisted with very indifferent results. Fully knowing that the cyathium is an inflorescence, modern botanists mostly stand wedded to the *Species Plantarum* of Linnaeus in which the cyathium is understood and used as a flower. If this be justified by the data at hand it is suggested that our method of studying the genus is not altogether on a par with the enormous increase of the knowledge of phylogeny, genetics, morphology, ecology and phytogeography that has taken place since 1753. Be it noticed: the issue of method, which is of the essence of investigation, cannot concern itself with the destiny of nomenclature although it must affect it profoundly. The conclusions of O. Schwarz and of Perrier de la Bathie, in the works cited above, afford evidence to support the thesis that both "unorthodox" and "orthodox" nomenclature are bound to heed the peculiar conditions of any given group of plants. No one may doubt at this hour that within a family are iron-clad genera representing the main phyla, and less well established genera that introduce segregates from these phyla. Thus the very name of genus is covering entities of avowed unlike weight, the value of which depends on the evolution of the whole aggregate under consideration. Hence the manifest impossibility of knowing the end of nomenclature before having fully explored the nature and the tendencies of a group of plants.

The cyathium of *Euphorbia* is an inflorescence, but, so far as the record teaches, it behaves in a manner wholly unbecoming the functions that an inflorescence is supposed to perform in taxonomy. The presence or the absence of "glands," the arrangement of the male and female elements,<sup>2</sup> the number of lobes in the calyxes, the position of the inflorescence and other less evident characters separate tribes and genera in the Euphorbia-

<sup>2</sup> As *male* and *female elements* are understood here the parts called by earlier botanists stamens and ovary, and by modern taxonomists male and female flowers. The classification of Euphorbiaceae is being hopelessly and needlessly confused by the use of the word "flower," now being applied to the male and female unisexual elements, then, again, to the uni- or biserial whorls of the uni- or bisexual perianth. Androecium and gynoecium also are liable to introduce conceptual confusion. The need for a better terminology of Euphorbiaceae was already by Baillon (1858), and a redefinition of our vocabulary in this respect is to be recommended as the subject of a bulky, most welcome thesis.

ceae. In *Euphorbia* as great, or greater, differences than these, even a dicocous instead of tricocous female element (cf. *E. Intisy*), leaves the genus unruffled and smilingly intact. What is this cyathium, this astounding performer?

The answer can be sought in either one of two ways. The cyathium can be studied *as it is*, or analyzed *as it was*. To elucidate: the cyathium can be dissected, its parts can be compared and its status generally tested in the light of principles that are accepted to indicate the age of live structures. At last defined as an old or a young organ the cyathium should tell whether its fickleness connotes active evolution or rapid degradation. It might transpire that the species of the genus are of different age and that it is possible to understand them in a logical, to say truly scientific age-sequence. This method considers the cyathium *as a unit*, in other words treats it as a flower. The point must be emphasized because it is plain from the testimony of the literature that it has never been obvious.

The method that investigates the cyathium as it was treats it as an *aggregate* of potentially adnate parts, to say an inflorescence. This treatment does justice to the known nature of the cyathium, and aims at mastering the process whereby it came into its present form, necessarily comparing it with the inflorescences of the whole family. If the relative age and importance of the component parts of the cyathium can be known the value of the cyathium itself is determined by a simple arithmetic addition.

Studied as it is what does the cyathium tell?

Hochstetter all too early and fleetingly to gain lasting credit thereby (1835), and Vavilov well supported by golden Sovietic ammunition (1931), have introduced and reformulated the concept of species as a system, indeed not a capital novelty to less illustrious authors who used *Gesammtarten* (Thellung, 1917). Fernald admits (1931) that age may be a factor of taxonomic ripeness in species of the same genera. E. J. Palmer accepts (1931), like Perrier de la Bathie (1932), the existence of outstanding species of which others are derivatives. So much authorizes the surmise that time is of the essence of living organisms, and that ancient structures are apt to be more sharply differentiated than recent ones. This suggests in turn that the amazing range of elusive variations existing in the component parts of the cyathium of *Euphorbia* is a sign of youthful exuberance. As time shall go by, probably, the cyathium will become stabilized along definite lines of evolution, and ultimately, which is much to be desired, shall come to rest in few neatly built mansions.

As it has been pointed out, however, a precisely contrary conclusion can be true. It may be that the cyathium having outlived its prime in eras long past is now headed toward the Elysian fields, therein to suggest

pertinent and impertinent controversies to the shadows of amused cynics and of cultured peripatetics. It is not impossible that the component parts of the cyathium are degenerating at different rates in the various species and groups of species of the genus. As time shall elapse the cyathium may further dwindle ending in nothingness, which, as things go, is certainly to be desired.

This issue of progress versus regress is one that the trained systematist forthwith recognizes as fundamental. Unfortunately, it is precisely the one that the cyathium studied as it is, and as a thing in itself, does not decide. Were the cyathium a power it could be discussed in terms of sympetaly and dialipetaly (McNair, 1935). But the cyathium is not a flower, and before the family in which it is found can be studied with good result something must be altered of classification which is now accepted as true. What may be known, barely, is that the cyathium is as old as the genera which it defines, but not old enough to have lost the powers of a very successful form of inflorescence. If the writer may be accused, with a show of good reason, of dismissing too lightly the advantages accruing from pulling the cyathium apart, it may not be doubted that masters who have studied it with anatomic zeal, Baillon, Boissier, Mueller Argoviensis, N. E. Brown, Hegi, Pax & Hoffmann have applied themselves, and made honest efforts. The results of such efforts require no comment. It is the inadequacy of the solutions so far proposed which leaves the subject on our hands to puzzle out.

What is the cyathium investigated as it was?

The answer requires the analysis of factors that are difficult, controversial, and to a very great extent not yet satisfactorily known. The very limits of this work forbid a fair treatment of the issues that must be considered, and comment on them should be withheld were it not that these notes are admittedly discursive: nothing that immediately affects nomenclature will be introduced here. In the hope that the sketchy data suggested in these lines can be elaborated in the future the writer presents his own opinions for what they are worth, mainly as a stimulus toward further much needed joint investigations.

The tendency of modern scientific works is mostly in the direction of a careful and presumed exhaustive study of one, or few points of fact. This tendency is justified in part by the very immensity of the field of modern knowledge, but only in part because it surrenders the achievement of the broad albeit not necessarily everlasting generalizations upon which rests the progress of thought. Mediaeval societies in which the sums of theology were silently prepared by colleges of monks may yet teach something to the modern world. Those valiant souls being wrapped up in celestial toils solved even the problems of the kitchen in terms of eternity.

Confused by graphs and partial reports, the botanist curious of Euphorbiaceae feels at last refreshed in stumbling into a work of Wettstein (1924) upon a fundamental statement of the issue of the classification of the family. Here are offered roomier chambers than those let out by Bessey (1897) whose *natural* classification (*Bessey's adjective, italics mine*) happens to rely upon what must be taken to be a single character.

Wettstein states that the issues presented by the classification of Euphorbiaceae are to be solved by the interpretation of the comparatively simple inflorescences of the family. If, quoth Wettstein, the constant unisexuality of the flowers (male and female elements, granted that the writer understands the subject correctly), the dominant apetalous perianth are archaic, then the Euphorbiaceae are Monochlamydeae (to say, a family of the group commonly accepted as "the lower orders"). If these same characters indicate the presence of regressive structures then the Euphorbiaceae must follow the Dialipetalae. Further Wettstein says: it appears that the Tricoccae, hence the Euphorbiaceae, belong to a plant-group of the organic order of the Monochlamydeae which has progressed in the direction of the Columnales, Gruinales, Therebintales, Celastrales (approximately Malvales, Geraniales, Sapindales of the classification of Engler & Prantl).

In the latter statement particularly Wettstein opposes organic structures to tendencies and to trends of evolution. If this dualism stands, the Euphorbiaceae have at the same time perianths (monochlamydeous wrappers), and true flowers (in this case dialipetalous floral structures).

Brought into sharp light this dualism is one that can be solved only with consideration of the trends of evolution of the whole family because these trends determine the true nature of *all* the floral structures of the Euphorbiaceae. In other words: the issue calls for the precise understanding of the limits of perianths and flowers. To elucidate: if a mere rearrangement of the parts and structures that are found, e.g., in the elongated floral axis of the Hippomaneae and Acalypheae has brought into being the structure, e.g., of *Wielandia*, which is spoken by modern systematists as of a true flower, it must be evident, weighty opinions to the contrary notwithstanding, that true flowers are lacking in Euphorbiaceae. Even the bisexual "flowers" of the family are more or less complex perianths, to say derivative structures to which the male and female elements have contributed, wholly or in part, the appurtenances (bracts, scales, calyxes, "glands," etc.) which were theirs in the ancestral phylum. Such "flowers," understood in function of what Pospichal (1897) happily calls the physiological momentum are not the same as the flowers, e.g., of *Nymphaea* in which the progression from petal to stamen in the floral whorl itself affords evidence to all the component parts having funda-

mentally evolved after, and not before their meeting within the floral whorl.<sup>3</sup> The difference may not be evident in morphology, and may escape the attention of the descriptive botanist because it involves *merely* an issue of concept. It is pregnant with meaning, however, to the systematist.

Assuming that perianths and true flowers both exist in Euphorbiaceae it is necessary to accept for a fact that the tendencies of the family run in opposite directions, precisely as Wettstein states. It follows that the entire classification of the group can make sense and be tolerably natural only after being written back to accomodate the "monochlamydeous" and the "dialipetalous" rumps of it. Surgery is unavoidable because the family is not well held together by the nature of the female element which has broad or narrow cotyledons (Platylobeae and Stenolobeae), is 1- or 2-ovulate (Phyllantoideae and Crotonoideae), and 2-20 or more-celled (*Hymenocardia* to *Hura*, through *Euphorbia*, *Dichostemma*, *Wielandia* etc.) Unfortunately, only tendencies are left for the systematist's work where morphology fails. Among our native species of *Croton*, *C. alabamensis*, having "flowers" with sepals and petals (Ferguson, 1901) will associate with the "dialipetalous" crowd leaving all other native species of the genus with the "monochlamydeous" section. Last but not least, if the Euphorbiaceae have both perianths and true flowers the cyathium of *Euphorbia* in no wise can correctly be distinguished and separated from the "flowers" of *Croton* [as represented by *C. alabamensis*] *Wielandia*, *Bridelia* etc. The "flower" of *Euphorbia* will be sympetalous precisely as that of the last named genera is "dialipetalous." Baillon (1858) clearly perceived, if only for a moment, the absurdities arising from the use of a double standard and it is irrelevant to the inherent soundness of his argument that he made of it the worst possible application. It is a foregone conclusion that if the Euphorbiaceae cannot have both perianths and true flowers, and they certainly number genera having perianths, *all the "flowers" of Euphorbiaceae are perianths.*

In fact the dualism of which Wettstein speaks appears to be pure illusion. Let us assume two elongated axes, one capped by a female element (ovary) with inferior spirally arranged fascicles of male elements (stamens) subtended each by a scale; the other ending with male elements and carrying a lateral inferior female element. Axes of this nature repre-

<sup>3</sup> It is not to be denied that even in perianths, *sensu omnium*, later adaptations of preexisting free parts can be safely traced back. The cyathium of *Euphorbia* is emphatically an adapted structure, as it will be seen later. The issue involved here, however, in principle is not as to what came *after* the perianth's formation, but as to what was *before* the coming into being of the perianth.

sent inflorescence-types widespread among Euphorbiaceae, and found, e.g., in Acalyphaeae and in Dalechampiaeae.

Let us now reduce to zero, or near-zero the length of the assumed axis. We see it, if ending with the female element, yield a central "ovary" surrounded by a whorl of "stamens" and by a "calyx." We have here, consequently, all the elements that are associated with a true actinomorphic flower, e.g., of Eleagnaceae. Through the same process of shortening, the axis that ends with male elements secures for us laterally opposed male and female "flowers", to say an inflorescence. To this might be reduced the dualism between monochlamydeous wrappers and dialipetalous structures supposed to exist in Euphorbiaceae: the position of the female element in the floriferous axis makes and unmakes the "flower" as soon as the axis itself is shortened. The very same component parts and an identic process are conducive to two structures that the eye perceives as different, and that are accepted as different in most of the current texts. It is probable that some misunderstanding is the root of the confused position of the family in modern systematic work. This fact is highly suggestive, that the systematists who give indication of being most undecided between flowers and perianths sooner than anybody else force the family into unnatural associations.

Knowing that the shortening of the axes carrying male and female elements might yield the floral structures (perianths and true flowers) supposed to coexist in the Euphorbiaceae, we have cause to look to the elongated axes of the Hippomaneae, Acalyphaeae etc., as to the structures that furnish the key to the understanding of the tendencies and the morphology of the inflorescences<sup>4</sup> of the entire family. These elongated axes are essentially amentaceous and unisexual, and connect very distinctly the Euphorbiaceae with the Monochlamydeae of Wettstein's classification. As a corollary it is to be inferred that the likeness of the "flowers" of *Bridelia*, *Cleistanthus*, etc., with the flowers of *Rhus*, *Celastrus* etc. bids fair to be accidental. Had the Anacardiaceae, Celastraceae, Dichapetalaceae lines of descent matching the Hippomaneae they should naturally be grouped with the Euphorbiaceae. Lacking these lines of descent the

<sup>4</sup> The value of this approach to the inflorescences of the whole family is not lessened, in the judgment of the writer, by the circumstance that the "flowers" of Euphorbiaceae may, or not be hermaphrodite on account of factors [e.g., altered metabolism] clearly not to be attributed to a process of actual shortening. It should be interesting to study the "branches" of *Phyllanthus* spp. and determine precisely whether they are anything but elongated leafy floral axes. Under the conditions that prevail in the family, and under the notions now current of it, it is almost impossible to generalize conclusions except in the broadest sense.



Anacardiaceae, Celastraceae, Dichapetalaceae, etc., take rank with the Dialipetalae of Wettstein. Palaeobotanists not less than morphologists and systematists may be interested in further investigating the matter.

Does the ovulation, which is often assumed as the main character of order and family classification, controvert the conclusion that the Euphorbiaceae are remote from the Geraniales of the classification of Engler & Prantl?

The question cannot be discussed here. It may be said, all too briefly, that the problem of surrounding a fertilized macrogamete with cellular tissues is analogous to the problem of inclosing space within four walls, a roof and a floor for the needs of habitation. The materials and the purpose being what mathematicians like to call a constant, or at least a limited quantity, the solutions may vary in detail remaining, however, fundamentally the same in all cases. Thus similarity and dissimilarity of form and structure need interpretation if they are to prove anything. Obviously, a successful interpretation must take into account every one of the factors inducing change of patterns. Hence rational systematic botany can never be established upon one static character, important is it may happen to be. The tendency, or cause, dominates the form, or effect.

So far in principle. In fact, granting that standard illustrations are correct (Payer, 1857) the Geraniales of Engler & Prantl embrace Malpighiaceae (*Malpighia urens*) in which the integuments of the ovule grow downwards, as in certain Proteaceae, and Geraniaceae (*Erodium serotinum*) in which the integuments grow, as in *Euphorbia*, upwards. Thus in the Englerian order the pendulous ovule with a ventral raphe is the finished product of opposite rhythms of growth. It takes an act of faith to believe that *Linum perenne* and *Stillingia sylvatica* have something in common, yet in the growth of the ovule of both the obturator-mechanism plays an important part, and, diagnostically, the obturator is of paramount value in deciding which plant belongs to Euphorbiaceae.

The ovule of the Euphorbiaceae is commonly believed to be anatropous, but Boissier (1862) and Mueller Argoviensis not less than Baillon (1858) describe it as anatropous or amphitropous, such, for instance, as it can be found in interesting aberrant forms (Mueller, 1873). Very characteristically, Ducke (1933) presents under Euphorbiaceae the genus *Polygonanthus* and debates its position between the former family and the Polygonaceae, while almost anything in the description and in the illustrations suggests the Olacaceae. In brief: sufficient data are gathered in the most cursory review to fortify the supposition that the ovulation of the Euphorbiaceae does not remove the family sufficiently far away from Moraceae, Urticaceae, Olacaceae, Polygonaceae to belie the tend-

encies that assimilate it with the true "ament orders" from which *Daphniphyllum* is assuredly not far remote (Hallier, 1904). It is only with the Monochlamydeae of Wettstein, and more or less in the position which Wettstein assigns to the family, that the Euphorbiaceae can come to rest, at least temporarily, if it be considered that they embrace *Phyllanthus*, *Jatropha*, *Hippomane*, *Hura*, *Euphorbia*, *Cubicolia*. Truly characteristic of the family are amentaceous inflorescences, connotating anemophily, which usually carry extensive nectaria and, often, bracts with manifest vessilliferous functions bespeaking entomophily. If the writer reads these characters correctly, here is observed a factual dualism which in its implication is far reaching: the family, in a way which is mostly of its own, has adapted anemophilous inflorescences to entomophilous functions, shortening axes, variously combining the appurtenances of the sexual elements, and the sexual elements themselves and reducing whole sets of male elements to nectaria.<sup>5</sup> Wettstein, once more, appears to be correct in establishing the Euphorbiaceae in an order fairly much of their own.

Let us now return to the elongated, fundamentally unisexual axis which we have assumed to test the dualism alleged to exist in the floral structures of the Euphorbiaceae. We may study this axis in three fundamentally distinct arrangements, as follows:

- 1) The male and female elements are on wholly distinct axes.
- 2) The male and female elements are on the same axis, the numerous male elements superior.
- 3) The male and female elements are on the same axis, the single female element apical.

Let us further assume that each one of these three forms of inflorescence is subjected to the same process which for the sake of brevity, if

<sup>5</sup> The issue anemophily versus entomophily records the following statement: "It seems very probable that extreme reduction of the perianth and consequent loss of attractiveness to insects would result in the adoption of another mode of pollen transference by the wind, *which in this case would not be a primitive condition*, as it undoubtedly is in the gymnosperms (Hutchinson's italics) (1926). Granted for the mere sake of hypothesis that an extreme reduction of the perianth has taken place in Euphorbiaceae, no loss of attractiveness to insects need result, because insects can be attracted by, a) scent. The violet-like odor of the cyathia of *Euphorbia esculenta* is distinct even to the obtuse turbinate of man. b) nectaria. These organs exist throughout the family, and whoever has seen them at work cannot doubt their efficacy. c) colored bracts and appendages. It is by no means certain that all insects react to colors as man does, but it is fairly certain that the bracts of *Euphorbia pulcherrima*, *E. polychroma*, *Dalechampia Roezliana* etc. have vessilliferous functions, for in the last two named species at least, they tend to discolor after anthesis. The zygomorphic cyathia of *Tithymalus* (*Pedilanthus*) give every evidence of being highly adapted ornithophilous or entomophilous structures.

not altogether correctly, we will call of exhaustion, and which is observed, e.g., at the apex of the floriferous stems in *Rhus glabra*. We can postulate: 1') both the male and the female axis are reduced in length, to say the number of the elements is reduced. This diminution does not change basically the numeric proportion of the elements, and does not effect, accordingly, the requirements of seed-fertility.

2') the male elements, being terminal, are sacrificed comparatively and absolutely to a much greater extent than the inferior female elements. This does not necessarily impair seed-fertility inasmuch as a single anther-cell usually yields many more gametes than a single ovary.

3') the female element being apical and single cannot be sacrificed without sterilizing the plant. It must be maintained lest the species be thrown back upon means of vegetative reproduction.<sup>6</sup> In the case under investigation the process that tapers off the inflorescence of *Rhus* must be substituted by other arrangements. There must be, in tendency, a readjustment of the vital balances of the plant, which is bound to take place between two given points, i.e., the apical female element and the cap of the longest rootlet. It will be seen that the problem met by the plant here is other than the problem offered in cases 1') and 2'), in which only *one* point is given, the apex of the floriferous axis being undeterminate, liable to shortening to various degrees.

In the phyla possessing an apical single female element a readjustment of vital balances caused by the process we have called exhaustion may be supposed to manifest itself at first in a shortening of the whole axis. This shortening should be accompanied by a suppression of non-essential axes, and by a general reduction in size of parts. The stems and branches of the plant may tend to develop essentially as inflorescence-bearing axes: hence, at least in the herbaceous and subwoody representatives of these phyla, a dominant cespitose or verticillate mode of growth, and a very unstable development of the whole plant independent of external conditions retarding or expediting the formation of inflorescences, to say of seeds. In brief: plants from these phyla may be supposed to have received a general impulse towards change and adaptation by virtue of the position of the female element.

<sup>6</sup> *Drosera* both in the American *D. rotundifolia*, and in the European *D. intermedia* may suffer degeneration of its carpellar structures, as noticed by Gates (1936), and at least in the former the var. *comosa* under certain conditions may prove to be better adapted to dominate its habitat than the seed-bearing type-species. This exception, although found to exist in the genus rather than in one species, does not infirm the rule that in higher plants sexual reproduction is favored against asexual reproduction. Very interesting in systematics is the fact that a manifest teratologic form can have the status of a good, viz., geographical and ecological variety, if only it is interpreted in relation to habitat and not otherwise.

*Euphorbia* belongs to a phylum in which the female element is apical. In it we observe, in fact: *a*) Shortening and suppression of axes. Precise note of this was made by Roeper (1824), R. von Veh (1928), Goebel (1931) and records to the same effect are found scattered in the literature, e.g., Hegi (1924), Lotsy (1928). *b*) Prevalence of cespitose and verticillate growth, manifest even in the largest species of the genus. *c*) Extended polymorphism, with the incidence of highly developed vernal and autumnal, luxuriant and depauperate forms, often very embarrassing to the taxonomist. *d*) Incidence of protective structures such as spines, which are adapted relicts of aborted axes. In *E. sect. Anthacantha* a whole umbellaster<sup>7</sup> becomes spinescent in *E. stellaespina*, and a solitary or ternate axis in *E. polygona*. *e*) Great difference between the main stem and the flower-bearing or sterile branches, the former often being reduced to characteristic "Medusa-head" shape (cf. *E. Caput-Medusae*, *E. sect. Anisophyllum*). *f*) General reduction in size of parts, most evident in succulent species.

It is not to be denied that analogous, or parallel alterations should be observed in species of all the phyla of the family in which the female element is apical, if the suggested hypothesis is correct. A definite answer, however, will be given only after the family is better known than it is at the present. In *Jatropha* that like *Euphorbia* extends to arid or semiarid zones, a close parallelism exists with the tendencies and structures of *Euphorbia*. However, *Euphorbia* alone in the family has adapted itself to the conditions that obtain at the opposite thermic poles of the earth, and it remains to be seen how the impulse arising from the position of the female element has exhausted itself in the genera, of the family which live under fixed climatic conditions. What may not be doubted at present is that all the tendencies and structures of *Euphorbia* operate, and take place in the presence of a cyathium, to say of a peculiar form of inflorescence, avowedly a shortened floral axis ending with a female element. It is also plain that Roeper perfectly understood the pulse of the genus, remarking that the tendency to shorten and to suppress axes dominates it. The acceptance of the existence of this tendency forthwith rationalizes *Euphorbia*, and every one of the structures of its species can be traced back to it.

Assured that *Euphorbia* tends to shorten its axes, and that the cyathium is a longitudinally reduced inflorescence, we may study the cyath-

<sup>7</sup> This term is proposed to take care of the "umbel" and "pseudoumbel" of the current literature on *Euphorbia*. The umbellaster is an aggregate of inflorescences *sui generis*, and is always technically to be distinguished from the true umbel in this that its central cyathium evolves first. The ending *aster* is not unknown in botanic terminology, existing in *verticillaster*, and in generic names like *Opulaster*, from *Opulus*.

ium reversing the process that brought it into being. Thus we secure once more an elongated axis along which nectaria (glands) and fascicles of male elements, subtended by a scale, are disposed in a spiral that may or may not have so definite a ratio as that announced by Schmidt (1907). The female element obviously is apical.

This ancestral axis has all the anatomic elements of *Stillingia* (e.g., *S. sylvatica*), and differs from the *Stillingia*-axes only in the position of the female element. The "missing fifth gland" that so much caught the fancy of Millspaugh (1898) is easily explained. The cyathium lacks true symmetry: projecting into a plane its ancestral axis we find as many "lobes" as there are fascicles, or groups of male elements. Five "lobes" and four "glands" result from an original spiral disposition in which the highest and lowest element of a series of nine alternate "glands" and "lobes" is a "lobe." Shifting the number and the position of the "lobes" and of the "glands" any kind of arrangement may be secured. The taxonomic possibilities thus arising will be explored in a later article.

In *Euphorbia* are known species with male elements surrounded or not by partitions (septa), with and without petaloid appendages, with and without "stipules" to the petiole, with cyathia evidently different in the degree of adnation of the component parts. In the Euphorbiaceae having elongated floral axes we know species in which the male elements are inclosed within a calyx (e.g., *Sapium longifolium*), or subtended by an open scale (e.g., *Actinostemon concolor*); genera in which calloused "stipules" and/or foliaceous stipules exist at various points of the blade and of the petiole (*Sapium*, *Omphalea*, etc.); species in which the "glands" near the female element carry evident lacinate structures ("sepals" in Baillon's *Adenopeltis Colliguaya*. In brief, we find in the species of *Euphorbia* every one of the characters found in species of the *Hippomaneae*, and entire "sections" of the genus in which these characters appear, or not. It logically follows that *Euphorbia* is a polyphyletic genus, the ancestral stems of which not only differed in the various parts that later became adnate to form the cyathium, but in the "stipules" as well. The cyathium cannot define the genus with rigor because it is an aggregate of structures that were unlike before adnation. Naturally, the presence or absence, and the nature of the "stipules" of *Euphorbia* have as great importance as the differences in the cyathium itself to indicate the polyphyletic origin of the genus. The tendency to shorten and to adapt axes which is as old as the inception of the tendency that brought the cyathium into being, has caused the *Euphorbia* of our herbaria to cover species in which the main axis (stem) has undergone profound hereditary alterations that have influenced in turn phyllotaxis, "stipules" and habit. So evident are there alterations that morphologists like Goebel and von Voh do not hesitate

fundamentally to oppose *E. sect. Anisophyllum* to the other species of the genus. Unfortunately, the hint seems to have been useless to taxonomists.

In conclusion: the cyathium of *Euphorbia*, correctly appraised, is younger than the tendency to shorten axes that dominate the genus, and younger than the "stipules" at the petiole. It may be assumed that the tendency to shorten axes is the result, or one of the main results, of the position of the female element in an elongated ancestral floriferous axis. This leads us back to Euphorbiaceae, the type-inflorescence of which is uni-sexual and amentaceous, which forbids their being associated with the Geraniales of Engler & Prantl. The bewildering variety of the three hundred genera of the family arises from the disposition or combination of male and female elements, together with their appurtenances, upon elongated uni- or bisexual axes. or within more or less highly evolute perianths, the fundamental unisexual tendency of the family often bringing about secondary abortion of male or female elements whenever the perianth is bisexual. The nectaria (glands) are indicated as degenerate, highly adapted clusters of male elements (stamens), with the petaloid appendage, if present, as the primary structure (Baillon, 1858). The "petals" and "sepals" of the "flowers" of certain genera are more definitely specialized vessilliferous bracts than the bracts, discoloring after anthesis of, e.g., *Dalechampieae* and *Euphorbiaeae*, or, which remains to be proved, enlarged sterile filaments (in *Poranthera*, fide Baillon). Troll's interpretation of the cyathium (Troll, 1928) obviously is worth notice as bibliography. It may be added that the amentaceous character of the type-inflorescence of Euphorbiaceae, associated with widely distributed nectaria and colored bracts, suggests that the urge variously to combine male and female elements, and to modify their appurtenances (calyxes, lobes, etc.) has probably been activated by a prevalent change from anemophilous to entomophilous pollination in an early stage of the evolution of the family.

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## Tolerance of liquid air temperatures by spore-free and very young cultures of fungi and bacteria growing on agar media

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(WITH ONE FIGURE)

In 1900, Macfayden and Rowland published results which made it seem highly probable that several species of bacteria and one yeast may withstand very low temperatures in a young vegetative state in liquid and solid media. The temperatures varied from liquid air temperatures (about  $-190^{\circ}$  C.) to liquid hydrogen temperatures (about  $-252^{\circ}$  C.). The exposures varied from a few hours to seven days. These facts are not only unknown to most microbiologists of today, but a number of those who are confronted with them doubt their finality. Owing to such skepticism and the following further considerations, the author of this paper determined to carry on some experiments in the same field in order to furnish more evidence to the scientific world relative to the questions at issue. The other considerations which led me to conduct my investigations were (1) that there was practically no evidence on the tolerance of low temperatures by young cultures of fungi in a fresh vegetative state except a short note by Kärcher published in 1931, and (2) that having myself published a series of papers (Lipman 1936a, b, 1934) on the tolerance by seeds, spores, and dry moss tissue of liquid air temperatures, it seemed wise to round out such a series of investigations by one dealing with the tolerance of liquid air temperatures by young vigorously growing fungi and bacteria on their characteristic media. In this connection, I did not overlook the impressive results of Zirpolo (1932) who proved that luminescent bacteria in a fresh vegetative state may withstand the temperatures of liquid helium (close to the absolute zero) for at least several hours without injury.

In view of the foregoing situation, I planned and executed two experiments which are described below.

### EXPERIMENT I

As shown in table 1, seven fungi and three bacteria were selected for study in the experiment. The fungi were selected from a larger number and variety because they showed no spore production in 24 hours. The bacteria were selected because they are non-spore formers in the microbiologist's sense of that term. Special emphasis was placed on using fungi in a spore-free stage for the reason that others, as well as the writer, had already shown that fungus spores can withstand, without injury, liquid-air temperatures and even temperatures close to the absolute zero; and



further because in most of Kärcher's fungus cultures, the possibility of resistance by spore substance rather than by vegetative substance may have been involved. Because of these considerations, all the fungi from which the selections were made were transferred each day for many days in order that I might assure myself by examination of the cultures relative to which ones were spore-free. Several species of fungi were not used in this experiment either because very little growth was obtained in 24 hours, or because there was a possibility that spores might be present. The medium for growing the fungi consisted of the following as given in Fred's Laboratory Manual of Soil Bacteriology:

Ammonium nitrate	10.0 grams
Diabasic potassium phosphate	5.0 "
Magnesium sulphate	2.5 "
Ferrous chloride	Trace
Saccharose	50.0 "
Distilled water	1000.0 c.c.
Agar	15.0 grams

This medium was used in culture test tubes and the fungi were grown on slants.

The medium used for the bacteria was standard bouillon agar.

The cultures thus prepared were sealed by drawing the open end of the test tube to a point in a flame and annealing. The sealed tubes were then placed in a metal container partly filled with lead shot to keep it from floating in the liquid air and the container was immersed in a large Dewar flask filled with liquid air. This was done at 11:00 A.M., 20th August, 1936. The cultures were removed from the liquid air at about 11:00 A.M. of the 22nd August, 1936, or 48 hours later. They were allowed to return to laboratory temperature gradually by wrapping the metal container, which still contained some liquid air, in several layers of absorbent cotton. This process of return to room temperature consumed several hours. The tubes were then unsealed and stoppered with sterile cotton stoppers, transfers were made from them to fresh media, and both original culture and transfers were incubated at 28° to 30° C. Slides were made of the treated cultures at the same time as the transfers, and these were examined immediately. The results obtained after incubation of the cultures and transfers for two weeks or more are given in table 1. The + sign stands for growth and the - sign for lack of growth.

It is clear from table 1 that all the bacteria tested and two of the fungi withstood without injury the temperature of liquid air for 48 hours, as judged by the macroscopically visible growth obtained in the treated cultures or in their transfers. In addition, however, microscopic examination

showed that on two of the slants showing no growth there was apparently healthy mycelium, namely in the original culture of *Aspergillus oryzae* and in the transfer of *Trichoderma* species. This is especially significant since the original culture of *Trichoderma* species yielded good growth after treatment and therefore the transfer thereof should have given the same result. It looks probable, therefore, that in some cases lack of macroscopically visible growth is not attributable to the annihilation of the fungus by the liquid air temperature but to other causes. This becomes more than a probability when the results in Experiment II below are studied and from other considerations. For example, it is in some cases necessary to use 24-hour cultures with just visible mycelial development for treat-

TABLE 1  
*Tolerance of liquid air temperature for 48 hours by fungi and bacteria*

LABORATORY NUMBERS	NAME OF ORGANISM	TREATED CULTURE	TRANSFER
1	<i>Aspergillus oryzae</i>	—	—
2	<i>Penicillium luteum</i>	+	+
3	<i>Rhizopus nigricans</i>	—	—
5	<i>Abisidia</i> species	—	—
6	<i>Mortierella</i> species	—	—
7	<i>Rhizoctonia</i> species	—	—
13	<i>Trichoderma</i> species	+	—
10	<i>E. typhi</i>	+	+
11	<i>S. enteritidis</i>	+	+
12	<i>B. coli</i>	+	+

ment by liquid air in order to avoid spore formation. But when the agar slant culture is exposed to liquid air it becomes markedly dehydrated and even broken perceptibly. The bit of mycelium with which we start may thus become completely buried in the agar and transfers made with the loop may miss the mycelium entirely and the latter in the original culture may be unable to make the growth in its submerged state. It is interesting to observe that when agar slants have been subjected to liquid air for 48 hours they not only show a tendency to break into two or three parts but also, even in unbroken specimens, show a dehydrated condition and a raised central ridge along the length of the slant. A photograph which accompanies this paper helps to make this matter clearer.

#### EXPERIMENT II

The results in Experiment I, taken together with the considerations in the discussion based thereon, rendered another and more elaborate experiment of this kind highly desirable. For that reason one was arranged which allowed of a larger selection of fungi and bacteria, and in many cases both 24-hour and 48-hour cultures were used. In no case, how-

ever, was a culture used in which spores were visible under magnification. Accordingly, twelve species of fungi were used in Experiment II and six new bacterial species since the results with the three species in Experiment I were conclusive. The media used in this experiment were as follows: For fungus cultures No. 6c, No. 7 and No. 8c, the same medium was used as the one employed for fungi in Experiment I. For the balance of the fungi, potato agar was employed as given in Fred's Laboratory Manual of Soil Bacteriology. It has the following composition:

Potato	200 grams
Agar	30 "
Dextrose	20 "
Distilled water	1000 "

For the bacteria studied the standard media were employed. Since these are well-known and universally used, they will not be described here.

The cultures were prepared and subjected to liquid air in the same manner as those of Experiment I. Exposure to liquid air was begun at 11 A.M. on the 26th October, 1936. The tubes were removed from the liquid air at 10:40 A.M. on the 28th October, 1936 (approximately 48 hours exposure). They were immediately placed in the refrigerator still surrounded by liquid air in the container, and kept there at about  $-5^{\circ}$  C. for three hours. They were then placed in an ice chest (temperature about  $+5^{\circ}$  C.) and left there over night. The next morning the tubes were unsealed, and transfers were made from all of them to fresh media. The original tubes and the transfers were then placed in the incubator at  $28^{\circ}$  to  $30^{\circ}$  C. except the cultures of *M. tuberculosis* (human and avian) and *Clostridium botulinum* which were placed in the  $37.5^{\circ}$  C. incubator. After two weeks or thereabouts, the cultures were carefully examined, and the results tabulated as given in table 2 which follows. Again, as in table 1, the plus and minus signs represent positive and macroscopically visible growth and no growth respectively.

The results set forth in table 2 leave no room for doubt as regards the essential correctness of the conclusions of Kärcher and Zirpolo which are cited above. They not only confirm the results given in table 1, moreover, but extend them markedly. We may now examine them more in detail and glean from them new lessons which they teach. It is clear from the second experiment as it was not from the first, that a change, sometimes a slight one, in the conditions of such experiment may yield results which are the reverse of those obtained without such a change. For example, whereas in the first experiment *Aspergillus oryzae* apparently was killed by liquid air temperatures it was not in the second experiment; the difference

TABLE 2

*Tolerance of liquid air temperatures for 48 hours by fungi and bacteria*

LABORATORY NUMBER	NAME OF ORGANISM	AGE OF CULTURE HOURS	TREATED CULTURE	TRANSFER	REMARKS
1	<i>Aspergillus oryzae</i>	48	+	—	
2	<i>Penicillium luteum</i>	48	+	+	
3	<i>Rhizopus nigricans</i>	24	—	—	
4	<i>Mucor species</i>	24	+	+	
5a	<i>Absidia species</i>	24	+	—	
5b	<i>Absidia species</i>	48	+	+	
6a	<i>Mortierella species</i>	24	—	—	
6b	<i>Mortierella species</i>	48	+	+	
6c	<i>Mortierella species</i>	24	+	+	Same medium as in Experiment I
7	<i>Rhizoctonia species</i>	48	—	—	Same medium as in Experiment I
8a	<i>Armillaria mellea</i>	48	—	—	
8b	<i>Armillaria mellea</i>	24	—	—	
8c	<i>Armillaria mellea</i>	48	—	—	Same medium as in Experiment I
9	<i>Aspergillus niger</i>	24	—	—	
13	<i>Trichoderma species</i>	48	+	+	
15a	<i>Pythium species</i>	24	—	—	Some growth shown under microscope
15b	<i>Pythium species</i>	48	?	?	Much growth shown under microscope
17a	<i>Fusarium species</i>	24	+	—	
17b	<i>Fusarium species</i>	48	+	+	
18	<i>Erwinia amylovora</i>	24	?	?	Much growth shown under microscope
19	<i>Erwinia carotovora</i>	24	?	+	
20	<i>Azotobacter chroococcum</i>	24	+	+	
21	<i>M. tuberculosis</i> (human)	—	+	+	
22	<i>M. tuberculosis</i> (avian or bovine)	—	+	+	
23	<i>Clostridium botulinum</i>	24	+	+	

between the two cases being that the culture was 24 hours old in the first and 48 hours old in the second experiment. Again, whereas in the first experiment *Mortierella* species was killed by liquid air temperatures in a 24-hour culture, it was not injured at all in a culture of the same age and on the same medium. Moreover, on the new medium, namely potato-dextrose agar, a 24-hour old culture apparently died at liquid air temperatures but a 48-hour old culture remained uninjured. Further, a 24-hour culture of *Absidia* species survived the liquid air treatment in Experiment II on potato-dextrose agar but did not do so in Experiment I on another fungus medium. That the slower return to normal temperature of the liquid air treated culture may account for the difference is certainly not improbable. But it is just as likely that that is only one factor in the

conditions which, when uncontrolled, may yield conflicting results in such experiments. On the other hand, *Rhizopus* and *Rhizoctonia* seemed to have fared as badly in the second as in the first experiment though the medium was varied for *Rhizopus* and the age of the culture for *Rhizoctonia*. Even these results, however, may not be taken as final because other factors like those discussed under Experiment No. 1 and others beyond my ken still may remain uncontrolled. In the case of *Armillaria mellea*, we have a fungus which grows so very slowly that its apparent failure to withstand liquid air temperatures may be explained by the fact that the little mycelium which it developed was completely submerged in the agar during treatment and could not emerge therefrom. In general, it seems to be a fact that 48-hour cultures withstand liquid air treatment better than 24-hour cultures and that cannot be explained on the basis of spore formation because there were no spores in sight at the time the cultures were exposed to the liquid air. A more reasonable explanation of this fact is that a change in the structure of the protoplasm occurs between the ages of 24 hours and 48 hours for the organisms in question, which renders them more resistant to extremely low temperatures. But this is stated without prejudice to other explanations which I have indicated above. I shall refer again to the nature of the possible change in the protoplasm on ageing which I have just mentioned. Out of twelve species of fungi, at least seven have survived the liquid air treatment, and out of nineteen fungus cultures (some duplicates), ten have survived. The facts can hardly be interpreted in any other way than that many fungi, and perhaps most of them, will tolerate liquid air temperatures for long periods. Whereas Kärcher found her cultures could stand liquid air temperatures for 13 hours, my cultures have shown such tolerance for a period nearly four times as long. This is especially impressive since I took special pains to use only fungus cultures which had no spores whereas some of Kärcher's cultures, as a study of her paper will show, may have contained a spore, or spores, as such.

Proceeding now to study the results obtained with the bacterial cultures in Experiment II, we find that they confirm beautifully the results in Experiment I. In fact, only one bacterium, *Erwinia amylovora*, gave no visible growth on the slants after subjection to liquid air temperatures and even in that case, scrapings from the slant showed numerous cells in an apparently living state which for some reason did not produce colonies. It is clear, therefore, that pathogenic as well as non-pathogenic bacteria, large as well as small cells, so far as tested, show a uniformly high resistance to low temperatures like those of liquid air. This seems to draw a

line of distinction between bacteria and fungi, if my results alone as given above are taken into consideration. Bacteria seem to be much more tolerant than fungi of extremely low temperatures. This conclusion must, however, be taken with a reservation in the light of the foregoing discussion.

#### GENERAL DISCUSSION

The kind of evidence presented in this paper as well as in the papers of Macfadyen, Kärcher, and Zirpolo, which I have cited above is of an entirely different nature from that given by myself and others on the tolerance of living matter in a resting or vegetative state (and very dry) to extremely low temperatures. Here we have evidence that living fungi and bacteria in the most active state of life with a full complement of water in the tissue and growing on a medium which is nearly all water can withstand liquid air temperatures and, in Zirpolo's experiment, temperatures close to the absolute zero. The fact that some fungi did not tolerate those low temperatures does not detract from the fact that other fungi and all or practically all of the bacteria tested did withstand those low temperatures successfully. This is the more true since the foregoing results indicate that negative results obtained with some of the fungi do not constitute a basis for a final judgment relative to the actual low temperature tolerances of the species or strains in question. In addition to the support given above for such a statement, I may point out, as I did in the case of *Erwinia amylovora*, a 48-hour culture of *Pythium* species showed, in scrapings from a slant which appeared to the unaided eye to have no growth on it, much apparently healthy mycelium and to a lesser extent the same was true of the 24-hour culture of *Pythium*. Most eloquent of all such comments is the following. The original culture of *Erwinia carotovora* showed, in scrapings from what appeared to the unaided eye to be a bare slant, many apparently healthy cells which did not multiply sufficiently to make visible growth on the slant, and yet a transfer from that culture gave heavy growth on the slant of the organism in question. We must leave to the future the full unrolling of the scroll which will tell us the whole story of this fascinating subject, but we may rest content that most, and perhaps all, bacteria and many fungi cannot be destroyed by extremely low temperatures under all conditions.

What can be the explanation of this extraordinary phenomenon in the light of what we know about the sensitivity of higher and of many lower plants to temperatures far higher than those under study here? My answer is a purely hypothetical one given only to stimulate discussion. It

is my view that the spaces between the colloidal micelles which make up the protoplasm of the fungi and bacteria in question are so tiny as to prevent dehydration of the cells to any extent through ice formation. The spaces being so very small, the effective pull of the protoplasm on the water molecules is great enough to overcome the pull of molecule of water for molecule of water as the temperature falls and the molecules of water attempt to orient themselves to make the pattern of the ice crystal. Hence the protoplasm, with its tightly bound water, to use a term which is unpopular in some circles, remains intact in its pattern as well as in its distended active state and survives the low temperatures under discussion. Were it not for this, speaking still hypothetically, the pattern of the protoplasm, and hence the organism, would be destroyed as it is in the case of cells with vacuoles and in the case of cells without vacuoles where the spaces between the micelles are much larger. In the case of dried plant matter like that of seeds and spores, and even dry moss, the pattern of the protoplasm remains intact, and hence it cannot be destroyed by low temperatures. In such forms of matter, however, resistance to low temperatures in the wet state will vary, in accordance with my hypothesis, with the sizes of the spaces between the colloidal micelles making up the pattern of its living substance.

While I have considered bacteria and fungi in this general discussion as if they were essentially the same in their resistance to low temperatures in the active state, I have a strong disposition to think from the facts at hand that bacteria are much more resistant than the fungi to extremely low temperatures and probably because their protoplasm provides a pattern with the smallest of all interstices between units or micelles of protoplasm, and hence contain water in the most perfectly bound form of any living organism of which we have knowledge. However, I do not wish to be taken to task for these hypothetical discussions and only give them to my colleagues to determine whether or not they are worthy of a hearing. I certainly do not desire to have these hypotheses detract from the striking facts which, in common with Macfadyen, Kärcher and Zirpolo, I have adduced in my studies, and which speak eloquently for themselves.

#### SUMMARY

1. Twenty-four and forty-eight hour cultures of several species of fungi and several species of bacteria in two experiments were exposed to liquid air temperatures on their normal agar media for 48 hours.

2. Eight out of twelve fungi showed ability to grow normally after such exposure.

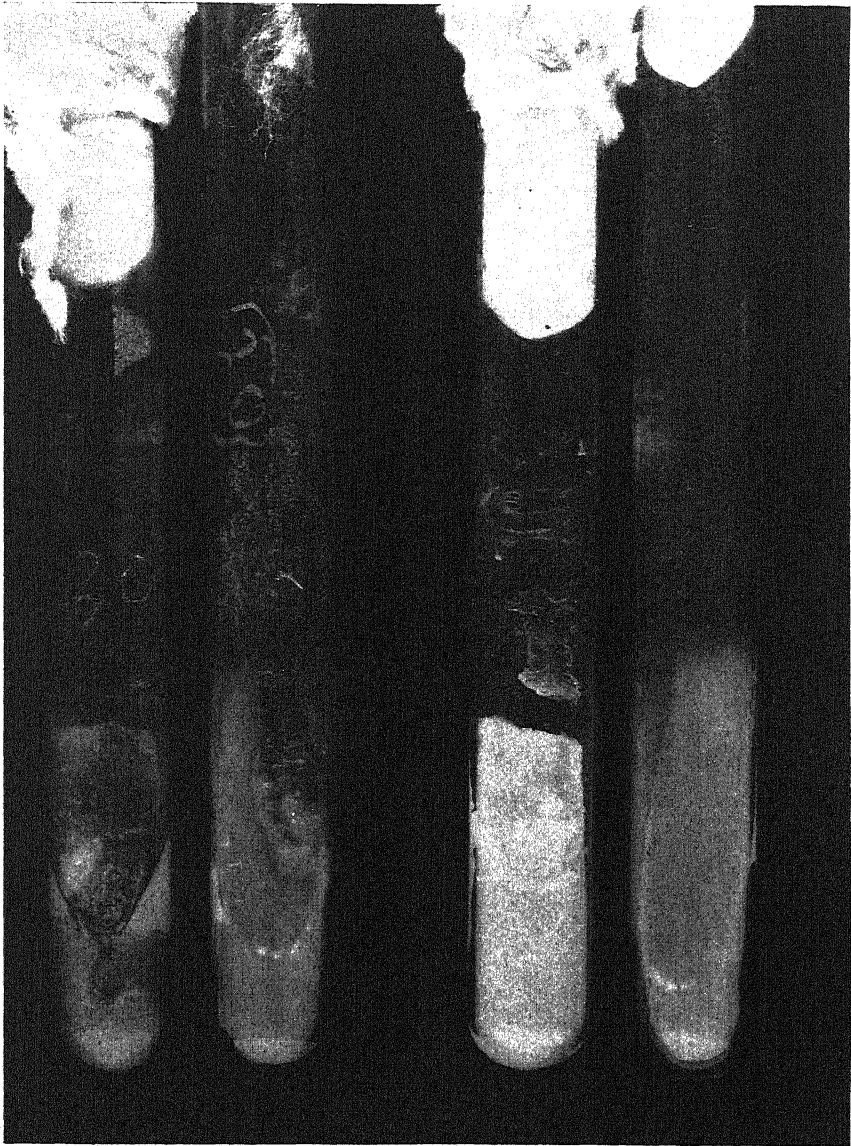


Fig. 1. Cultures from experiments on tolerance of liquid air temperature by vegetative forms of fungi and bacteria. Left to right: First two tubes *Azotobacter chroococcum*; second two tubes, *Erwinia amylovora*. The first tube of each pair was exposed to liquid air for 48 hours. The second tube is a transfer from the first tube after exposure. The broken condition of the agar slant following exposure to liquid air is shown in the first and third tubes.



3. All bacteria except one made copious growth on agar slants after such exposure. The one exception showed growth on the slant microscopically but not macroscopically.

4. The significance of these findings is discussed and a hypothesis for explaining them proposed.

5. These experiments confirm similar experiments for fungi by Kärcher, and for bacteria by Macfadyen and Zirpolo.

My warm thanks are extended to my faithful research assistant, Mr. W. L. Chandler, for his valuable help and to Dr. C. W. Porter of the Chemistry Department of the University for furnishing the liquid air used in the experiment.

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## New plants from the Yucatan peninsula<sup>1</sup>

C. L. LUNDELL

The 1936 botanical expedition of the Carnegie Institution of Washington and the University of Michigan to British Honduras undertook botanical studies from June through August on the limestone plateau and in the granitic Mountain Pine Ridge of El Cayo District. Scores of plants new to the flora of British Honduras and Central America were discovered. New species described on the following pages represent in part the novelties found on the expedition. Two new plants are described from the 1936 British Honduras collections of Dr. Hugh O'Neill of the Catholic University of America.

*Ficus guajavoides* sp. nov.—Arbor, 45 m. alta, glabra; stipulae lanceolatae, 2.8–4.5 cm. longae, acuminatae, glabrae, deciduae; petioli crassi, 2.5–6 cm. longi; laminae ovaes vel suborbiculares, 10–20 cm. longae, 8–14.5 cm. latae, apice basique rotundatae, coriaceae, punctatae, costa prominenti, 3–4.5 mm. lata, nervis lateralibus 11–17-jugis; receptacula solitaria, 1.8–3.5 cm. longe pedunculata, subglobosa vel obovoidea, 2–2.7 cm. diam., glabra, verrucosa.

A large tree, height 45 m., diam. 75 cm., with low thin buttresses and smooth round trunk, entirely glabrous; branchlets thick; stipules lanceolate, 2.8 to 4.5 cm. long, acuminate, glabrous, deciduous; petioles thick, 2.5 to 6 cm. long; leaf blades oval or suborbicular, broadest at the center, 10 to 20 cm. long, 8 to 14.5 cm. wide, rounded at apex and base, coriaceous, punctate, very prominently veined, the veins whitish beneath, the costa 3 to 4.5 mm. wide, the lateral veins large, 11 to 17 on each side, divergent almost at right angles, nearly straight, anastomosing to form a submarginal vein; peduncles thick, 1.8 to 3.5 cm. long; receptacles solitary, subglobose or obovoid, 2 to 2.7 cm. in diameter, somewhat verrucose.

Type in the Herbarium of the University of Michigan, *C. L. Lundell* 6295, collected in high advanced forest near Valentin, El Cayo District, British Honduras, June 29, 1936.

The species is closely related to *F. Tonduzii* Standl. from which it is distinguished by larger stipules, oval-orbicular leaves rounded at apex (not apiculate), and larger number of lateral veins. The receptacles resemble fruits of *Psidium Guajava* L.

*Coccoloba mayana* sp. nov.—Arbor, 8–15-metralis; ramuli puberuli; ochreae 3.5–8 mm. longae, rufo-tomentellae, apice barbatae; petiolis 6–10 mm. longis; folia ovato-ovalia vel oblongo-ovalia, 5.5–12 cm. longa, 3–7 cm. lata, coriacea, apice apiculata vel rotundata, basi subcordata, glaberrima, primum subtus ad costam minute puberula, punctata, minute reticulato-

<sup>1</sup> Contribution from the Herbarium of the University of Michigan.

venosa; inflorescentia terminalis, racemosa, 8–24 cm. longa, puberula, nodulis 1–2-floris; bracteae abbreviate orbiculares, ca. 1 mm. longae, 1.2 mm. latae, puberulae; ochreolae membranaceae, bracteam subaequant, puberulae; pedicelli bracteam subaequant; perianthii tubus obconicus, basi stipitiformiter contractus, ca. 2.3 mm. longus, lobis suborbicularibus, ca. 2 mm. longis; stamina ca. 2.4 mm. longa, erecta, antheris exsertis; ovarium ellipsoideum, trigonum, 1.4–1.8 mm. longum; styli 3, 0.5–0.75 mm. longi; fructus ovoideus, 8 mm. longus, 5 mm. diametro.

A tree, height 8 to 15 m.; young twigs densely puberulous striate; stipules 3.5 to 8 mm. long, thin, brittle and densely puberulous at first, thicker and rufous-tomentose with age, bearing tufts of long red hairs at apex; petioles 6 to 10 mm. long, shallowly canaliculate, densely puberulous; leaf blades ovate-oval or oblong-oval, 5.5 to 12 cm. long, 3 to 7 cm. wide, coriaceous, apex apiculate or rounded, base shallowly cordate, unequal, glabrous except for a few minute hairs beneath along the costa, densely punctate, with 6 or 7 pairs of lateral nerves, finely reticulate-veined; inflorescence terminal, racemose, 8 to 24 cm. long, the rachis minutely puberulous, reddish, nodes 1- or 2-flowered; bract subtending flowers depressed-orbicular, about 1 mm. long, 1.2 mm. wide, minutely erose and rounded at apex, minutely puberulous; ochreolae suberect, membranous, nearly equaling or slightly longer than bract, minutely puberulous or nearly glabrous; pedicels of flowers equaling or slightly exceeding bract in length; perianth tube obconical, constricted at base into a short stipe, about 2.3 mm. long (including stipe), punctate, glabrous; perianth lobes suborbicular, about 2 mm. long, punctate, glabrous; stamens erect, about 2.4 mm. long, exserted; ovary narrowly ellipsoid, trigonal, short-stipitate, 1.4 to 1.8 mm. long; styles 3, 0.5 to 0.75 mm. long; stigma fleshy, minutely nodulose; fruits sessile, the pedicels only slightly exceeding ochreolae in length, ovoid, 8 mm. long, 5 mm. in diameter, longitudinally sulcate.

Type in the Herbarium of the University of Michigan, *C. L. Lundell 1498* (flowers), collected on the bank of the Rio San Pedro de Martir above El Paso, Department of Petén, Guatemala, April 17, 1932.

Additional specimens examined: Guatemala: Department of Petén: La Libertad, *Lundell 3212, 3230, 3340; Aguilar 275, 313* (fruit).

The species was found only in wet soils on river banks and around *aguadas*. *C. mayana* is related to *C. Schiedeana* Lindau from which it differs in having longer racemes, nodes 1- or 2-flowered, larger flowers, and sub-orbicular perianth lobes.

***Phoebe longicauda* sp. nov.**—Arbor, 8-metralis, ramulis junioribus rufopilosis; petiolis 4–10 mm. longis; folia lanceolata vel lanceolato-elliptica, 3.5–11 cm. longa, 2–4.5 cm. lata, apice caudato-acuminata, basi acuta, sparse pilosa, subchartacea; inflorescentia pauciflora, paniculata, 1–4.5 cm. longa, breviter pilosa, pedicellis 2–3 mm. longis, bracteolis deciduis; perianthii tubus sub-

nullus; limbi segmenta subaequalia, ca. 3 mm. longa, anguste elliptico-obovata vel oblongo-spatulata, apice obtusa, intus breviter tomentosa; filamenta antheris breviora, pilosa, seriei III glandulis binis; antherae quadrilocellatae, subrectangulares; staminodia ser. IV conspicua, sagittata, stipitata, filamentis pilosis; ovarium glabrum; bacca ellipsoidea, nigra, ca. 1 cm. longa.

A small tree, height 8 m., diam. 7 cm.; young branchlets coarsely rufous-pilose; petioles 4 to 10 mm. long, glabrescent with age; leaf blades lanceolate or lanceolate-elliptic, 3.5 to 11 cm. long, 2 to 4.5 cm. wide, caudate-acuminate, the acumen obtusish, oblique, base acutish, sparsely pilose on both surfaces, glabrescent with age except along the costa, finely reticulate veined, subchartaceous; inflorescence few-flowered, paniculate, axillary or subterminal, 1 to 4.5 cm. long including peduncle, the branches sparsely short-pilose; pedicels 2 to 3 mm. long, sparsely short-pilose, the bracteoles deciduous; perianth segments subequal, about 3 mm. long, tomentose inside, less hairy outside, the 3 outer lobes narrowly elliptic-obovate, the 3 inner lobes oblong-spatulate, slightly shorter than outer lobes, apex obtusish; stamens of series I and II introrse, the filaments less than one-half length of anthers, short-pilose, the anthers 4-celled, subrectangular; stamens of series III subextrorse, the filaments about one-half length of anthers, pilose, biglandular, the glands subsessile, anthers 4-celled, laterally dehiscent, subrectangular; staminodia of series IV prominent, sagittate, the filaments pilose; ovary glabrous; berry ellipsoid, black, about 1 cm. long; cupule small, shallow, red.

Type in the Herbarium of the University of Michigan, *C. L. Lundell 6833* (flowers), *6757* (fruit), collected in riparian and marginal forest near San Agustin, Mountain Pine Ridge, El Cayo District, British Honduras, August 1936.

Additional specimens examined: British Honduras: El Cayo District: Valentin, *Lundell 6401*; vernacular names "*aguacatillo*." In jungle beyond Little Mountain Pine Ridge, *Bartlett 13098*. Belize District: Gracie Rock on the Sibun River, *Gentle 1572*. Stann Creek District: All Pines, *Schipp 571*.

The caudate-acuminate leaves, short few-flowered inflorescence, and tomentose perianth segments distinguish the species.

*Calliandra rivalis* sp. nov.—Frutex, 3–7 m. altus; rami teretes glabrescentes; stipulae triangulari-subulatae, ca. 3 mm. longae, striatae; folia 0.8–2 cm. longe petiolata, pinnis 1-jugis; foliola  $1\frac{1}{2}$ -juga, anguste lanceolata vel oblanceolato-elliptica, 2–5.5 cm. longa, 0.8–1.6 cm. lata, subcoriacea, apice breviter obtuso-acuminata vel obtusa, costa supra sparse puberula; inflorescentiae 1–2.3 cm. longae pedunculatae; bracteae ca. 0.8 mm. longae; calyx ca. 2 mm. longus, 5-dentato-apiculatus; corolla 7 mm. longa, lobis ovatis, acutiusculis, ca. 2.1 mm. longis; filamenta 3–3.5 cm. longa; legumina 14–17 cm. longa, ca. 8 mm. lata, apiculata, longe attenuato-stipitata, puberula.

Shrub, height 3 to 7 m.; twigs terete, glabrous or with a few scattered hairs; stipules triangular-subulate, 3 mm. long, striate, persistent; petioles 0.8 to 2 cm. long, pilose on upper side; pinnae 1 pair; leaflets  $1\frac{1}{2}$  pairs, narrowly lanceolate or oblanceolate-elliptic, 2 to 5.5 cm. long, 0.8 to 1.6 cm. wide, oblique, short obtuse-acuminate or obtuse, glabrous except for a few hairs on upper side of midrib, subcoriaceous, obscurely reticulate-veined, dull; peduncles 1 to 2.3 cm. long, wine-colored, sparingly covered with short glandular hairs; bractlets about 0.8 mm. long; flowers red, glabrous except for a few scattered short glandular hairs; calyx about 2 mm. long, 5-dentate-apiculate; corolla 7 mm. long, the lobes ovate, acutish, about 2.1 mm. long; filaments 3 to 3.5 cm. long, the tube somewhat exerted; legume 14 to 17 cm. long, about 8 mm. wide, apiculate, narrowed below the middle into a long tapering stipe, puberulous.

Type in the Herbarium of the University of Michigan, *C. L. Lundell* 6610, collected in the rocky bed of Rio Frio at San Agustin, Mountain Pine Ridge, El Cayo District, British Honduras, July 26, 1936.

**Tephrosia belizensis** sp. nov.—Herba erecta, perennis, 40–75 cm. alta, caulibus sulcatis, hirsutis; folia 8–17 cm. longa, breviter petiolata vel sessilia, rhachi sulcata, hirsuta; foliola 5–15, lanceolata vel ovato-lanceolata, 2–6 cm. longa, 0.7–2.1 cm. lata, apice acuminata, basi obtusa, supra glabra, subtus dense strigosa; inflorescentiae racemosae, terminales vel axillares; bractae linearilanceolatae, quam 7 mm. breviores; calyx dense fulvo-pilosus, tubus ca. 3.5 mm. longus, lobis inaequalis, lanceolatis, 2–5 mm. longis; corolla 1.3–1.6 cm. longa; stylus pilosus; legumina 6–7 cm. longa, ca. 6 mm. lata, brunneo hirsuta.

A slender erect perennial, 40 to 75 cm. high; stem sulcate, silvery-hirsute or somewhat brownish; leaves 8 to 17 cm. long, short-petioled or sessile; rachis sulcate, hirsute; leaflets 5 to 15, lanceolate or ovate-lanceolate, 2 to 6 cm. long, 0.7 to 2.1 cm. wide, apex acuminate, base obtuse, glabrous dark green and shining above, densely silvery-strigose beneath, the lower pair of leaflets ovate-oval, much reduced; racemes terminal and axillary; bracts linear-lanceolate, about 7 mm. long or less; calyx densely fulvous-pilose, the tube about 3.5 mm. long, the lobes very unequal, lanceolate, attenuate, 2 to 5 mm. long, persistent; corolla 1.3 to 1.6 cm. long; banner suborbicular, short-clawed, fulvous-pilose without; wings oblanceolate; style pilose, incurved; pods 6 to 7 cm. long, 6 mm. wide, brown-hirsute.

Type in the Herbarium of the University of Michigan, *C. L. Lundell* 6662, collected on the open rocky bank of Rio Frio near San Agustin, Mountain Pine Ridge, El Cayo District, British Honduras, July 29, 1936.

Additional specimens examined: British Honduras, El Cayo District: Mountain Pine Ridge, border of ravine, *Bartlett* 11588; flowers magenta.

The species is closely related to *Tephrosia submontana* (Rose) Riley. It differs most obviously in the smaller flowers and pods.

***Zanthoxylum nigripunctatum*** sp. nov.—Arbor, 27-metralis; ramuli puberuli; folia pinnata, foliolis 3–9, rachi puberula; foliola oblongo-elliptica vel oblanceolata, 2.5–10 cm. longa, 1.5–3.7 cm. lata, basi inaequaliter acuta, apice breviter angustata, acumine obtuso, subchartacea, sparse puberula, subtus nigripunctata; inflorescentiae terminales vel axillares, paniculatae; quam 10 cm. breviores, ramis puberulis; florum femineorum calyce 1.2 mm. lato, 5-dentato, puberulo; petalis 5, oblongi-ellipticis vel elliptici-lanceolatis, 2.4–3 mm. longis, 1–1.2 mm. latis, obtusis, glabris; gynaeceum globosi-obovoideum, carpellis 3 vel raro 4, punctatis, basi connatis; stigma subsessile, peltatum, ca. 1.3 mm. diam., triangulare, leviter 3-lobatum.

An unarmed tree, height 27 m., diam. 40 cm.; young twigs, rachis of the leaves and branches of the panicles puberulous with simple hairs; leaves even-pinnate, or odd-pinnate, 9 to 22 cm. long, the rachis deeply sulcate; leaflets 3 to 9, commonly 6 to 9, oblong-elliptic, the terminal leaflets oblanceolate, the basal leaflets much reduced, 2.5 to 10 cm. long, 1.5 to 3.7 cm. wide, base unequal and acutish or cuneate, apex short acuminate, the acumen oblique and obtuse, subchartaceous, obscurely crenulate, shining above, paler beneath, and black-punctate, prominently but finely reticulate-veined and very sparsely puberulous on both surfaces; panicles terminal or axillary, less than 10 cm. long; pistillate flowers: calyx puberulous, about 1.2 mm. wide, 5-dentate, the teeth triangular, acutish, about 0.3 mm. long; petals 5, oblong-elliptic, or elliptic-lanceolate, 2.4 to 3 mm. long, 1 to 1.2 mm. wide, apex blunt and thickened, yellow-green, glabrous; staminodia 5, rudimentary; gynaeceum globose-obovoid, 3- (rarely 4-) carpellary, the carpels punctate, united at base; stigma subsessile, peltate, about 1.3 mm. in diameter, triangular, shallowly 3-lobed.

Type in the Herbarium of the University of Michigan, *C. L. Lundell* 6487, collected in advanced forest south of Cohune Ridge, El Cayo District, British Honduras, July 12, 1936; vernacular name "prickly yellow."

Apparently related to *Zanthoxylum arborescens* Rose and *Z. melanostictum* Cham. & Schlecht., two imperfectly known Mexican species.

***Trichilia erythrocarpa*** sp. nov.—Arbor, 20 m. alta, ramulis, petiolis, et rachibus novellis dense pubescentibus; folia 12–30 cm. longa, 2–7 cm. longe petiolata; foliola 7–10, alterna, oblonga vel oblongo-elliptica, 4.5–13 cm. longa, 1.5–5.3 cm. lata, apice acute acuminata, basi rotundata, obtusa, vel acuta, juniora sparse pilosa, adulta glabriuscula; petioluli 3–5 mm. longi; paniculae axillares, sessiles vel subsessiles, 2.5–12 cm. longae, minute pilosae; calyx acute 5-dentatus, minute pilosus; petala 5, oblongo-ovata, ca. 2 mm. longa, 1 mm. lata (in floribus juvenilibus), minute sericea; filamenta (in floribus juvenilibus) in tubum 0.5–1 mm. longum connata; antherae oblongae,

sessiles, cum denticulis alternantes; stylus ovario brevior; stigma cylindricum; capsula rubra, oblonga, 1.6–2 cm. longa, dense puberula.

A tree, height 20 m., diam. 25 cm.; twigs, petioles, and rachis densely pubescent, the hairs somewhat appressed; leaves 12 to 30 cm. long, even or odd-pinnate, petioles and rachis nearly terete or slightly sulcate above, the petioles 2 to 7 cm. long; leaflets 7 to 10, alternate, oblong or oblong-elliptic, 4.5 to 13 cm. long, 1.5 to 5.3 cm. wide, apex acuminate, base rounded, obtuse, or acute, sparsely pilose on both surfaces at first, densely so along the costa beneath, glabrescent with age, the costa and lateral nerves prominent beneath; petiolules 3 to 5 mm. long; lower leaflets smaller, ovate-oblong; panicles axillary, 2.5 to 12 cm. long, often about as wide as long, branching from the base, the branches somewhat flattened and more or less grooved, short pilose; flowers pinkish, sessile or with pedicels 1 to 3 mm. long; calyx 5-dentate, the teeth acutish, short-pilose; petals 5, oblong-ovate, about 2 mm. long, 1 mm. wide in immature flowers, minutely sericeous; anthers in immature flowers oblong, about 1 mm. long, sessile, the staminal tube 0.5 to 1 mm. high, bearing 1 or 2 acuminate teeth between the anthers, glabrous; ovary hirsute; style short; stigma large, cylindric; capsule 3-valved, reddish, soft and pulpy when ripe, oblong, 1.6 to 2 cm. long, densely puberulous with short somewhat appressed hairs; aril orange-red; 1-seeded, the seeds about 11 mm. long.

Type in the Herbarium of the University of Michigan, *C. L. Lundell 6495*, collected in advanced forest on limestone hillside near Cohune Ridge, El Cayo District, British Honduras, July 13, 1936.

Additional specimens examined: British Honduras: El Cayo District: Valentin, *Lundell 6319, 6364*.

The species is distinguished by the pilose leaves, small flowers, and red pulpy fruits.

***Acalypha Mortoniana*** sp. nov.—Frutex, 1.5–4 m. altus, ramulis adpresso-pilosis; stipulae setaceae, ca. 5 mm. longae; petioli 0.7–11 cm. longi, graciles, pilosi; lamina ovata, 9.5–25 cm. longa, 4–13.5 cm. lata, apice acuminata, basi breviter cordata vel rotundata, juniora sparse pilosa, adulta glabriuscula, membranacea, crenato-dentata; spicae masculae axillares, 5–16 cm. longae; spicae femineae terminales, 10–12 cm. longae; bractae abbreviate orbiculares, sub anthesi 5–6 mm. longae, 6–8 mm. latae, sub fructu 9 mm. longae, 16 mm. latae; sepala ovato-lanceolata, acuminata, ca. 2 mm. longa; ovarium sparse hirsutum; capsula ca. 5 mm. longa; semina obovoidea, ca. 4 mm. longa.

A slender erect shrub, 1.5 to 4 m. high; branchlets appressed-pilose; stipules setaceous, about 5 mm. long; petioles 0.7 to 11 cm. long, slender, pilose, glabrate with age; leaf blades ovate, 9.5 to 25 cm. long, 4 to 13.5 cm. wide, apex acuminate, base shallowly cordate or rounded, at first sparsely pilose on both surfaces, especially along the veins, glabrescent with age, membranous, margin crenate-dentate or subentire; staminate spikes axillary, 5 to 16

cm. long, bearing only staminate flowers; pistillate spikes terminal, many-flowered, 10 to 12 cm. long; bracts depressed-orbicular, 5 to 6 mm. long, 6 to 8 mm. wide, retuse-cuspidate, the margin subentire, glabrous inside, with long gland tipped hairs outside and along the margin, accrescent, becoming shallowly bilobed-cuspidate, 9 mm. long, 16 mm. wide, with about 10 acute teeth; sepals ovate-lanceolate, acuminate, about 2 mm. long, sparingly pilose, the marginal hairs glandular; ovary smooth, sparingly hirsute with ascending hairs; styles hairy, with numerous ascending filiform branches; capsule about 5 mm. long, smooth, glabrous except for a few scattered appressed hairs; seed obovoid, smooth, about 4 mm. long.

Type in the Herbarium of the University of Michigan, *H. H. Bartlett 12740*, collected at Uaxactun, Department of Petén, Guatemala, April 25, 1931.

Additional specimens examined: Guatemala: Department of Petén: Yaxha-Remate road, *Lundell 4095*. British Honduras: El Cayo District: Valentin, *Lundell 6203* (fruit).

The shrub is common in forest on the calcareous uplands, especially in the vicinity of Valentin. It is named for Mr. C. V. Morton who studied some of the material cited.

***Myginda Gentlei*** (Lundell) comb. nov. *Rhacoma Gentlei* Lundell, Carnegie Inst. Wash. Publ. 478: 212. 1937.<sup>2</sup>

***Myginda puberula*** (Lundell) comb. nov. *Rhacoma riparia* var. *puberula* Lundell, Carnegie Inst. Wash. Publ. 478: 213. 1937.

***Myginda riparia*** (Lundell) comb. nov. *Rhacoma riparia* Lundell, Carnegie Inst. Wash. Publ. 478: 213. 1937.

***Calyptranthes fluviatilis*** sp. nov.—Frutex 2–3 m. altus, ramis junioribus rufo-tomentellis; folia 5–10 mm. longe petiolata, coriacea, lanceolato-linear, 5.5–8 cm. longa, 1–1.9 cm. lata, apice longe caudato-acuminata, basi cuneata, supra glabra, juniora subtus tomentosa, matura glabrata; inflorescentiae terminales, paniculatae, 3.5–7 cm. longae (pedunculo incluso), rufo-tomentosae; flores sessiles; alabastra obovata, ca. 3 mm. longa, rufo-tomentosa; petala desunt, ut videtur nulla; stamina numerosa; ovarium biloculare.

A shrub, height 2 to 3 m.; young twigs, branches of the inflorescence, and petioles rufous-tomentose, glabrate with age; petioles canaliculate, 5 to 10 mm. long; leaf blades lanceolate-linear, 5.5 to 8 cm. long, 1 to 1.9 cm. wide, apex long caudate-acuminate, the acumen slightly oblique to falcate, base cuneate, coriaceous, glabrous above, at first tomentose beneath, glabrate with age, costa impressed above, prominent beneath, lateral nerves small, numerous, parallel; inflorescence terminal, 3.5 to 7 cm. long including peduncles, panic-

<sup>2</sup> Since these species were described the writer has undertaken the revision of *Rhacoma* and related genera. The species may be satisfactorily referred to *Myginda*.



ulate; flowers white, sessile; buds obovate, about 3 mm. long, rufous-tomentose; perianth tube campanulate; apparently apetalous; stamens numerous; ovary 2-celled, with 2 ovules in each cell; immature fruits globose, 5 mm. in diameter, glabrescent with age.

Type in the Herbarium of the University of Michigan, *H. H. Bartlett 12949* (flower buds), collected at El Cayo, El Cayo District, British Honduras, April 16, 1931.

Additional specimens examined: British Honduras: El Cayo District: El Cayo, *Lundell 6117* (fruit).

A common shrub growing at the river edge above El Cayo. It is related apparently to *C. Lindeniana* Berg.

***Calyptanthus O'Neillii* sp. nov.**—Arbor glabra; folia 10–16 mm. longe petiolata, lanceolata vel oblongo-lanceolata, 10–14 cm. longa, 3–4.5 cm. lata, apice longe acuminata, basi acuta, subcoriacea; inflorescentiae axillares, subumbellato-paniculatae, 2–3.5 cm. longae (pedunculo incluso); flores subsessiles; alabastra obovata, 4–5 mm. longa, glabra; petala desunt, ut videtur nulla; stamina numerosa, 3–7 mm. longa; stylus 4–5 mm. longus.

A tree, glabrous throughout; branchlets slender, drying black; petioles 10 to 16 mm. long, slender, drying black; leaf blades lanceolate or oblong-lanceolate, 10 to 14 cm. long, 3 to 4.5 cm. wide, apex long acuminate, base acute, costa impressed above, conspicuous beneath, lateral nerves numerous, parallel, subcoriaceous; inflorescence axillary, subumbellate-paniculate, 2 to 3.5 cm. long including peduncles, about as wide as long; flowers glabrous, subsessile, drying black, subtended by triangular, acutish bracteoles; buds obovate, 4 to 5 mm. long; perianth tube infundibuliform; apparently apetalous; stamens numerous, 3 to 6 mm. long; style 4 to 5 mm. long.

Type in the Herbarium of the University of Michigan, *Hugh O'Neill 8764*, collected in an old clearing about 7 kilometers northwest of Belize, Belize District, British Honduras, August 21, 1936; fruits purple.

***Eugenia cocquericotensis* sp. nov.**—Frutex, ramulis gracilibus, novellis sparse puberulis, subcompressis, internodiis 1.5–3 cm. longis; folia 3.5–5 mm. longe petiolata, oblongo-elliptica vel lanceolato-elliptica, 3.5–7.5 cm. longa, 1.5–3 cm. lata, apice caudato-acuminata, basi acuta, subchartacea, juniora supra minute puberula, subtus glabra, sparse punctata; inflorescentiae axillares, racemosae, 1.2–2.3 cm. longae, sessiles, 3–11-florae, minute puberulae; flores sessiles vel brevissime pedicellati; alabastra ca. 3 mm. diam.; calyx glaber; sepala 4, subaequalia, breviter suborbicularia, 1–1.7 mm. longa, ca. 2 mm. lata, ciliata, punctata; petala 4, obovata, 4–5 mm. longa, ca. 3 mm. lata, apice rotundata, punctata, glabra, ciliata; stamina numerosa, 2–4 mm. longa; ovarium glabrum, biloculare; ovula in quoque loculo 2–3; stylus ca. 5 mm. longus.

A shrub; twigs grayish-brown, somewhat flattened, slender, sparsely puberulous, internodes 1.5 to 3 cm. long; petioles 3.5 to 5 mm. long, canaliculate, sparsely puberulous with somewhat appressed hairs; leaf blades oblong-elliptic or lanceolate-elliptic, 3.5 to 7.5 cm. long, 1.5 to 3 cm. wide, apex caudate-acuminate, the acumen narrow attenuate acute, base acute, subchartaceous, at first minutely puberulous above especially along the costa, glabrous beneath, sparsely punctate, margin obscurely crenulate, costa impressed above, prominent beneath, the lateral nerves anastomosing to form two inconspicuous marginal veins; inflorescence axillary, racemose, the racemes 1.2 to 2.3 cm. long, sessile, 3-11-flowered, minutely puberulous; flowers sessile or subsessile; pedicels about 1 mm. long or less, each subtended by an ovate acute punctate ciliate bract 1 to 2 mm. long; flower buds about 3 mm. in diameter; calyx glabrous, the sepals 4, unequal, depressed orbicular, 1 to 1.7 mm. long, about 2 mm. wide, ciliate, punctate; petals 4, obovate, 4 to 5 mm. long, about 3 mm. wide, apex rounded, punctate, ciliate; stamens numerous, 2 to 4 mm. long; ovary 2-celled, with 2 or 3 ovules in each cell, glabrous; style about 5 mm. long.

Type in the Herbarium of the University of Michigan, *C. L. Lundell 4090*, collected in secondary growth at Little Cocquericot, Belize River, El Cayo District, British Honduras, June 1933.

The species is distinguished by small acuminate leaves, elongated racemose inflorescences, sessile or subsessile flowers, and ciliate sepals and petals. It has been confused with *E. Capuli* (Schlecht. & Cham.) Berg. from which it is clearly distinct. It is related apparently to *E. yucatanensis* Standl., a species known to the writer only from the original description.

***Eugenia O'Neillii* sp. nov.**—Frutex ramosissimus, 1.5-2 m. altus; rami hornotini plus minus compressi, breviter pilosi, internodiis 1-2 cm. longis; folia 2-3.8 mm. longe petiolata, lanceolata vel anguste lanceolato-elliptica, 2.5-5.5 cm. longa, 0.6-1.9 cm. lata, apice longe acuminata, basi abrupte acutiuscula vel acuta, subchartacea, juniora supra minute puberula, matura glabriuscula, subtus glabra, punctata, sed costa primum breviter pilosa; flores in axillis fasciculati, subsessiles, pedicellis 0.5-1.8 mm. longis, puberulis; calyx glaber, punctatus, lobis brevissimis, rotundato-truncatis, minute tomentellis; petala latissime ovata, ca. 1.3 mm. longa; 1.5 mm. lata, punctata, minute tomentella; stamina numerosa, ca. 3 mm. longa; ovarium biloculare; stylus 4-5 mm. longus.

A much-branched shrub, 1.5 to 2 m. high; twigs red, very slender, somewhat flattened, puberulous or short pilose, internodes 1 to 2 cm. long; petioles 2 to 3.8 mm. long, short pilose; leaf blades lanceolate or narrowly lanceolate-elliptic, 2.5 to 5.5 cm. long, 0.6 to 1.9 cm. wide, apex long acuminate, the acumen narrow obtuse or acutish, base abruptly acutish to acute, at first

minutely puberulous above, especially along the costa, glabrous beneath except for a few hairs along the costa, glabrescent with age, punctate, sub-chartaceous, costa prominent beneath, the lateral nerves nearly obsolete; flowers fascicled in the leaf axils, subsessile, the pedicels 0.5 to 1.8 mm. long, puberulous; calyx tube glabrous, punctate, the lobes very short, rounded-truncate, minutely tomentulose inside and around the edges outside, the tube splitting at anthesis; petals depressed orbicular-ovate, about 1.3 mm. long, 1.5 mm. wide, sometimes with a short claw, punctate, minutely tomentulose inside and outside, especially around the edges; stamens numerous, about 3 mm. long, ovary 2-celled; style 4 to 5 mm. long, sparsely pilose at base.

Type in the Herbarium of the University of Michigan, *Hugh O'Neill* 8767, collected in mangrove swamp 4 kilometers north of the Sibun River and about 12 kilometers south of Belize, Belize District, British Honduras, August 24, 1936.

Additional specimens examined: British Honduras: El Cayo District: Mountain Pine Ridge, among granite boulders in the bed of Rio On, *Lundell* 6803.

The species is distinguished by its red twigs, small leaves, and subsessile fascicled flowers.

***Strychnos hirtiflora*** (Standl.) comb. nov. *Strychnos panamensis* var. *hirtiflora* Standl., Field Mus. Bot. 11: 138. 1932.

From several collections recently obtained it is evident that the variety should be given specific rank.

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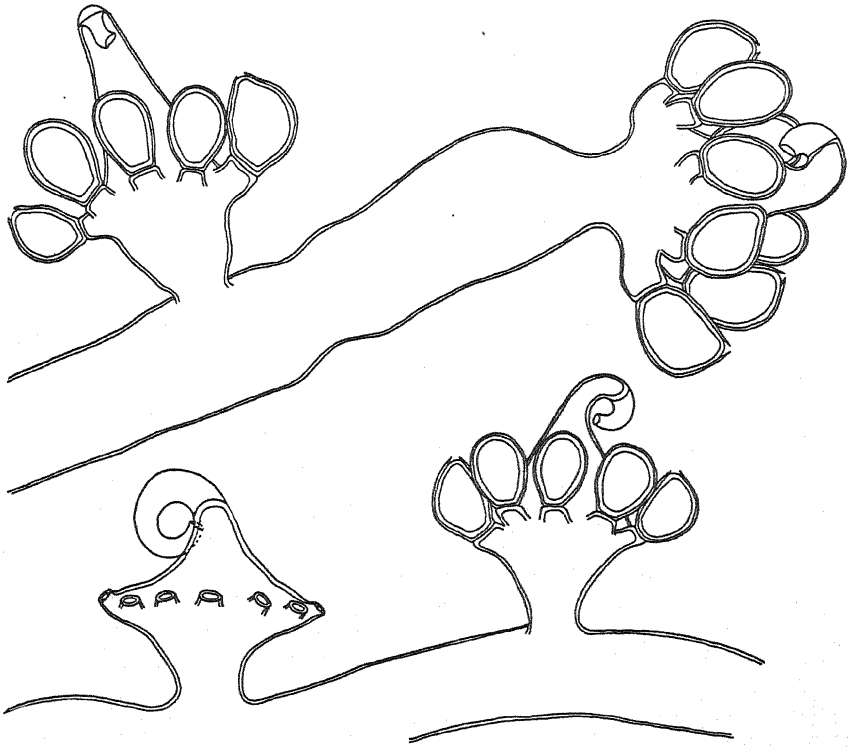
## A new species of *Vaucheria*<sup>1</sup>

CLARENCE E. TAFT

### *Vaucheria discoidea* sp. nov.

Oogoniis plerumque 8, forma variantibus ab ovoidea ad oblongam-ovoideam, obliquis, stipitatis circum peripheriam expansionis discoideae brevium ramorum lateralium; oosporis eadem forma ac oogoniis, et complementibus oogonia; membrana coriis 2; antheridio 1, circinato.

Filaments 110–170 $\mu$  diam.; oogonia six to sixteen, normally eight, ovoid to oblong-ovoid, more or less oblique, stipitate about the periphery



of a disc-like expansion of the short lateral branches, 64–90 $\mu$   $\times$  78–92 $\mu$ ; disc sometimes terminal on the main filament; oospores the same shape as the oogonium and completely filling it, 62–90 $\mu$   $\times$  78–90 $\mu$ , membrane of two layers, the outer thick and smooth, the inner thin and wrinkled; antheridium one, rarely two, circinate, on a pedicel above the center of the disc, 34–44 $\mu$  diam. Floating in quiet water. Miami, Oklahoma. The important diagnostic character of this species is the disc which bears the unusually numerous oogonia.

<sup>1</sup> Paper from the Department of Botany, Ohio State University. No. 382.

## INDEX TO AMERICAN BOTANICAL LITERATURE 1935-1937

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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# The fundamental nature of the flower<sup>1</sup>

JOHN H. SCHAFFNER  
(WITH PLATES 12 AND 13)

In 1925 the writer published a general account of the evolution of the flower<sup>2</sup> in which the subject was covered in a general way; but since some rather fantastic notions have recently been advanced about the origin and evolution of the angiospermous flower it was thought proper to present a further statement with the addition of certain facts and principles which must be taken into account in any comprehensive treatment. In the previous paper also no distinction was made between the epigynous flower with a tubular, epigynous hypanthium and the epigynous flower with a solid, epigynous hypanthium. With the recognition of the latter type, there are then nine fundamental, morphological types of flowers. The primary causal factor in the evolution of the flower is determinateness of the reproductive axis. If the reproductive axis of a vascular sporophyte is indeterminate, the plant is a flowerless plant. Thus the flower is definitely defined, as a determinate sporophyll-bearing shoot, or a modification of such a shoot.

The sporophyte of the Bryophyta is a radially symmetrical system and the embryonic sporophyte of the vascular plants also develops a radially symmetrical or cylindrical axis with a hemispherical mass of meristematic cells at the upper end from which lateral appendages or leaves are produced, originally in acropetal succession. The terminal bud may have a single apical cell or a group of initial cells but the development of the axis and lateral appendages results in either case in the same fundamental type, a cylinder with the leaves arranged in definite spirals when development is complete. The growing stem bud, whether terminal or lateral, is fundamentally indeterminate in growth, as appears in such simple types as *Lycopodium lucidulum* Michx. or *Osmunda cinnamomea* L. This is in marked contrast to the extreme determinateness of the sporophyte of liverworts and mosses in which the terminal bud of the sporophyte is destroyed by the reproductive process. We are not immediately concerned as to how the system of lateral appendages, including the sporophylls, was originally evolved from a stem system without appendages, but we must be cognizant of the fact that the living vascular plants from the ferns, horsetails, and clubmosses on up to the very highest angiosperms have evolved and retained the potentiality of spiralization in the production of lateral appendages with practically no exceptions.

<sup>1</sup> Papers from the Department of Botany, The Ohio State University, No. 388.

<sup>2</sup> Schaffner, John H. Principles of Plant Taxonomy II. Ohio Jour. Sci. 25: 219-243. 1925.

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Fundamentally then the flower is of essentially the same nature as the vegetative shoot.

As intimated above, the reproductive process in the living vascular plants has been shifted from the stem tissues themselves to the leaves and thus the growing bud in the lower forms produces alternate zones of purely vegetative or foliage leaves and sporophylls in an indefinite succession. The production of reproductive zones or rosettes is present in *Psilotum*, in the lowest species of *Lycopodium*, in all the ferns, in the quillworts, in the carpellate plants of the genus *Cycas*, and in both carpellate and staminate plants of *Ginkgo*. In *Psilotum* there is a distinct difference between the leaves with sporangia in their axils and those without. Although the reproductive branches are determinate sooner or later, this determinateness is vegetative, like the vegetative determinateness in the branches of the higher species of *Lycopodium*, and commonly the production of sporangia has ceased sometime before growth of the branch ends, or there may be more than one reproductive zone produced. All other higher, vascular plants have determinate reproductive shoots or flowers. The reproductive reactions initiate processes which sooner or later bring about complete stopping of growth and death of the given bud. The introduction of this new, reproductive, determinate potentiality constituted the evolution of the flower and the potentiality was evolved independently in a number of phyletic lines of vascular plants. There is then no difficulty in determining whether a plant has flowers or not, since both the physiological conditions and the morphology of the flower are clearly defined. At the lower levels of the evolution of reproductive determinateness of the stem axis, stopping of growth takes place very slowly and indefinitely. Thus the number of sporophylls is not only large but varies greatly from flower to flower, while in the highest flowers determination is very prompt and definite. Because of the extreme promptness of determination and consequent shortening of the cell lineage, in the extreme types of flowers, the differentiation processes are often confused and many of the structures are so modified that it is often difficult to homologize them with the more normal organs of the primitive flowers. Unfortunately these extremely reduced and specialized flowers have often been considered to indicate direct relationships and to be directly derived from each other, when they really represent phylogenetic culminations of independent evolutionary lines. Thus it has been assumed that *Juniperus*, *Ephedra*, *Casuarina*, *Juglans*, etc. form a progressive phylogenetic line of relationship. To one accustomed to consider the evolution and taxonomy of the plant kingdom from the geological and phyletic point of view, such an arrangement seems exceedingly fantastic and un-

reasonable, since all lines of fundamental study point to evolution as an irreversible process.

On the lowest levels of floral evolution the potentiality for determinateness is not decidedly perfected and thus failure of the reaction or proliferation is frequent, as in species of *Lycopodium*, *Equisetum fluviatile*, *Selaginella*, *Araucaria*, *Cunninghamia*, *Rosa*, and other genera. The lower flowers are appropriately called strobili or cones and these two words should be used synonymously, but a strobilus should never be called a spike. Since flowers appear in two classes of homosporous pteridophytes it follows that the lowest are homosporous or neutral flowers. There is no sexual dimorphism in any lycopod or equisetum flower. But in the heterosporous plants sexual dimorphism is always present either between parts of the same flower or of separate flowers. Heterosporous flowers are bisporangiate or monosporangiate; if monosporangiate they are megasporangiate or microsporangiate and in the seed plants they should be called carpellate and staminate flowers respectively. Monosporangiate flowers may be evolved from bisporangiate flowers through a change in the time of sex determination. In these flowers vestiges of the opposite set of sporophylls are usually developed to a greater or less degree, but in extreme cases they are completely suppressed. There is a second possible mode of evolution for some monosporangiate flowers, which may have been the mode in some gymnospermous strobili. A monocious condition of the reproductive branches may have evolved before the determinate reproductive potentiality or flowers and a branching tree produced with alternating sporophylls and vegetative leaf zones and with different sexual states determined on different twigs. Now if the reproductive determinateness was introduced into such a system it would result directly in monosporangiate flowers and such flowers would show no vestiges of the opposite sporophylls. This may have been the sequence, in the evolution of the flowers of the ordinary conifers which show no vestiges of the opposite secondary sexual structures. This is in marked contrast to the monosporangiate flowers of most angiosperms together with a few gymnosperms, like *Welwitschia*, which show vestiges in the vast majority of cases either in one flower or in both. Of course, it is well known that occasionally bisporangiate flowers occur in various conifers, but these are plainly the result of accidental sex reversal and not a recapitulation of a more primitive condition.

The strobilus type of flower may show a decided disturbance in the transition zone between the vegetative and reproductive zones of the shoot, but the transition characters are for the most part much less extreme than in the angiosperms. Hereditary potentialities may be

evolved which come into play in the transition zone and give rise to peduncles, branching reactions resulting in inflorescences, simple perianths, and involucre. One or more of these characters may be observed in various species of *Equisetum*, *Lycopodium*, and *Selaginella* and also in the gymnospermous cycads, conifers and joint-firs. A definite, sterile perianth or calyx is present in the higher species of *Equisetum* and prominent involucre are present at the base of the pedicels of the staminate flowers of *Taxus* and of both staminate and carpellate flowers of *Ephedra*, *Welwitschia* and *Gnetum*. The lowest types of flowers are developed at the ends of ordinary vegetative shoots as in *Equisetum*, *Lycopodium annotinum* L., *Araucaria*, and *Magnolia*. The next step in the evolution of floral position is the axillary flower, as in *Macrozamia*, and *Asimina*.

Inflorescences result from a branching factor active in the reproductive bud and from differentiations and shortening of the inflorescence branches. The main axis below the branching system may also be involved, giving rise to such extreme angiospermous inflorescences as the heads and discs of the Compositales, the syconium or fig fruit, and the cyathium of surges.

#### THE FLOWER OF ANGIOSPERMS

The most highly evolved flowers are found in the Angiospermae which contain a single phylum, the Anthophyta. The angiospermous flower is, however, fundamentally the same system as that of the strobili of horsetails, clubmosses, cycads and conifers. In the lower levels the flowers are essentially merely more elaborated strobili, as can be seen in *Echinodorus*, *Magnolia* and *Myosurus*. Probably the most advanced feature is the perianth which is usually very conspicuous in the lower types of angiosperms. The flowers are fundamentally radially symmetrical systems with lateral organs developed in spirals. The pitch of the clockwise and counter-clockwise spirals becomes equal in the more advanced forms and the parts are then developed in cycles and vertical ranks. The cyclic condition is frequently present in the perianth even if the sporophylls are still in the more primitive spiral arrangement. It will be remembered that very primitive flowers may be completely cyclic as in *Equisetum*. The angiospermous flower is fundamentally a bisporangiate system and this fundamental type may be changed to a monosporangiate condition by the progressive shifting, to an earlier stage of the ontogeny, of the time of sex determination, to the axis below the flower, as in the various kinds of monociousness and dieociousness.

The older systems of classification of the Dicotylae were based on the development and modification of the perianth, especially on the corolla, and the main divisions were thus Polypetalae, Monopetalae and Apetalae, or in the more recent Engler system Archichlamydeae (*Apetalae* and *Chori-*

*petalae*) and Metachlamydeae or Sympetalae, which amounts to the same thing. But this gave only a very artificial arrangement, since there are many families and even individual genera that contain species represent-

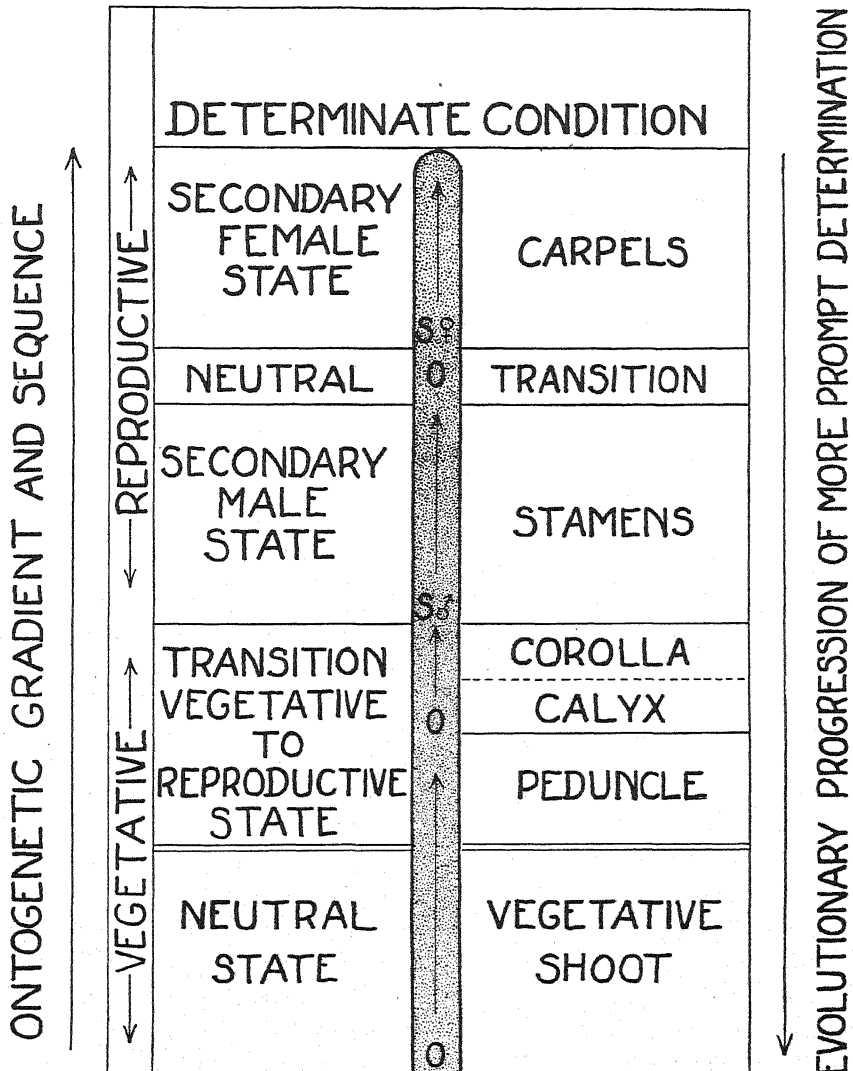


Chart 1. Diagram illustrating the general nature and development of the primitive flower of the angiosperms.

ing all the three general types. A much more fundamental morphological system is obtained by taking into account the general progressive determination of the floral axis and its expansions or other modifications.

The general nature of the development of the primitive angiospermous flower is illustrated in chart 1. As the floral bud approaches and passes through its determinate growth a definite growth gradient is developed and in consequence a definite series of activities is carried out from the beginning to the end. As the bud passes from the neutral or vegetative condition to the reproductive phase, it produces first a peduncle and then a perianth. Next, along with the reproductive reactions, the secondary male state appears and this is followed by a neuter transition zone as the bud reverses to the secondary female state, in which it normally remains until determination is complete. The neutral transition between the male and female conditions is usually so abrupt that no special developments appear. In some cases, however, a prominent internode may develop as in *Michelia* and species of *Geum* or special bracts may develop, different from both sepals and petals, as in *Aquilegia*.

The general, progressive evolution of determinateness together with the expansive growth factors operative in the floral axis have produced the fundamental morphological flower types. The determinateness of the flower bud may be brought about in two general ways. The entire mass of cells of the flower bud may stop growth uniformly or the central part of the bud may stop growing while the cortical region continues growth for a time, giving rise to the epigynous types of flowers. The expansive factors of the floral axis are active in association with the secondary sexual states developing in the axis. A careful study of living forms as well as a consideration of the possibilities under this evolutionary system show that there are nine fundamental, morphological flower types in the angiosperms. It must always be remembered that there are often transition types between the nine normal types but for the most part the types are easily recognized. There may also be more than one type of flower on a single plant.

The general ontogenetic and phylogenetic or evolutionary activities of the flower may then be reduced to a few general potentialities and summarized as follows:

1. The primary potentiality which is the cause of flower production is the determinateness of the floral axis in relation to the beginning of the reproductive reactions of a shoot. In the primitive flower types, the determination acts very slowly and indefinitely, producing a wide degree of fluctuation in the floral members. The general evolution of the flower then in all the phylogenetic lines is to a more prompt and more definite determination of the floral axis until the possible limit is reached. As stated above, the determination of the flower bud may be differential, the center of the bud stopping growth before the cortical region does. In

the extreme epigynous types the ovulary represents mainly cortical or cauline tissues, only the top with the style and stigmas and the partitions, if such are present, being cortical outgrowths or vestigial sporophylls. In the lowest flowers all the parts are usually entirely distinct but as determinateness of the floral axis advances and cell lineages are shortened, union of parts generally appears, usually first in the gynecium followed by unions in the perianth and finally all the parts may be more or less united. There is, so to speak, a telescoping of the processes of cell development and cell differentiation, and although other factors may be involved the fundamental cause appears to be especially associated with the determinate process, since no such union of parts is shown by any of the very primitive flowers, even though the plant may already have united leaf sheaths, as in *Equisetum*.

2. Hereditary factors may be evolved in the cell which have an expansive action on the flower bud as a whole or in the basal region of the floral axis which is passing into the secondary male state, or in the terminal region which is passing into the secondary female state. Such expansions may appear in the secondary male tissues of either the hypogynous or epigynous flower types, giving rise to a hypogynous hypanthium (perigynous disc) or to an epigynous hypanthium. The epigynous hypanthium must be distinguished from the ordinary perianth tube.

3. There may be adnation between the hypanthium and ovulary in the case of perigynous flowers or between the hypanthium and style, resulting in a solid growth above the ovulary in the case of epigynous flowers. This adnation is accomplished by the introduction of a factor which causes intercalary growth in the neutral transition tissues between the tissues in the secondary male state and those in the secondary female state, as in the adnate hypogynous hypanthium of the apple, and the adnate or solid epigynous hypanthium of the iris.

The interaction of these three general growth factors accounts for all the fundamental morphological flower types, and as stated above an inspection of the possibilities indicates that there can be nine types and no more. It is possible for each of the nine flower types to be developed as a radially symmetrical system or to be modified to a zygomorphic or bilateral condition through the determinateness of the bud or hypanthium developing more promptly on one side than on the other, and thus establishing peculiar physiological gradients around the flower bud which influence the expression of the shape, size, color, etc. of the general floral organs. In rare cases an isobilateral condition may evolve and zygomorphy may be superimposed on this potentiality as in *Capnoides*, or an inequilateral potentiality may be added to the zygomorphy, as in *Marantaceae*.

In addition to the general structural conditions, the flower may be modified in three general subordinate ways.

1. There may be a partial or complete suppression of one or the other sets of sporophylls (stamens or carpels) through the shifting of the time of sex determination to some point below the beginning of flower production. The same conditions may be present in the various types of monocious and diecious plants. The size or the absence of the vestiges will depend on the promptness and intensity of development of the secondary sexual states in the incipient tissues involved. In some cases both sets of sporophylls may become vestigial by the introduction of a hereditary factor which inhibits the development of both the secondary male state and the secondary female state in the flower, giving rise to a neutral condition.

2. There may be numerous genes evolved in the cell which give rise to complex chemical reactions with the production of various chemical compounds as pigments, odors, color patterns, deliquescent substances, etc.

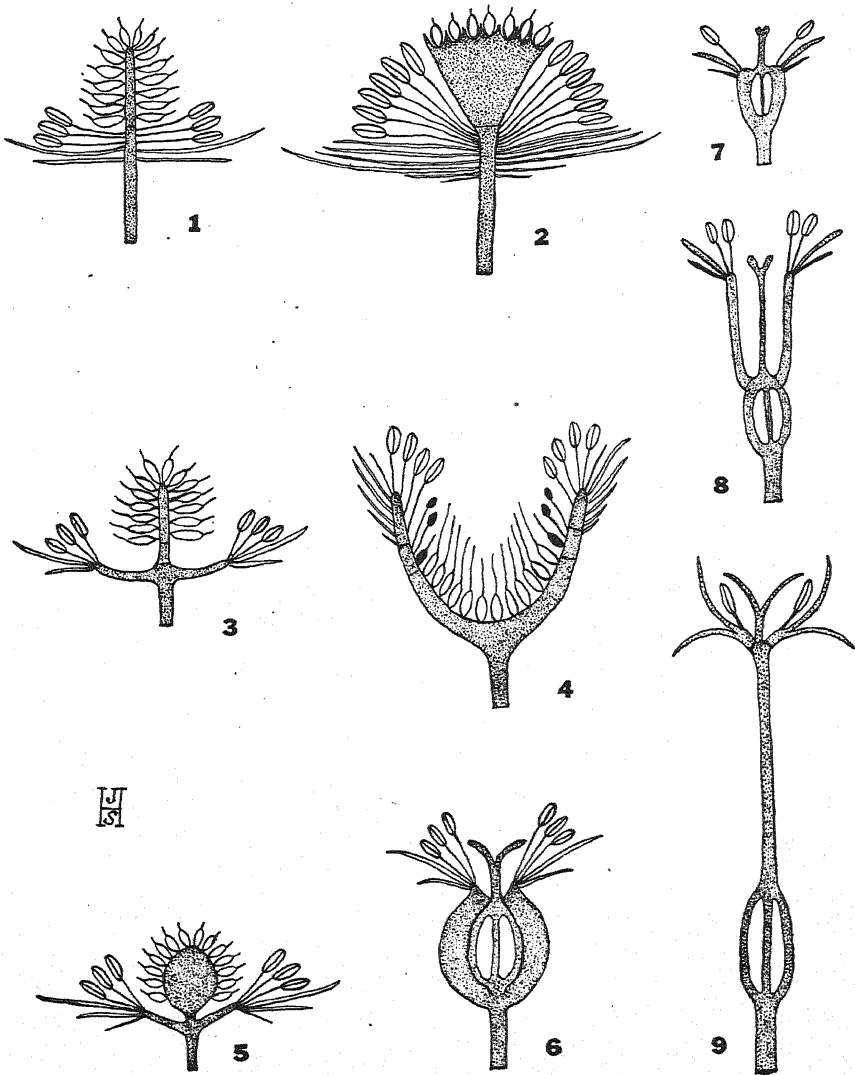
3. There may be hereditary factors or genes modifying the growth of the size, shape, surface appendages, etc. of the floral organs including the sepals, petals, stamens, and carpels and special glands. In some extreme types of floral evolution the structures may become very fantastic and complicated as in some Burmanniaceae and Orchidaceae.

In 1916, the writer published a short paper on a method of constructing floral diagrams and gave graphs representing the five most common types of flowers.<sup>3</sup> This method has been found satisfactory for phylogenetic studies of the flower. Below a complete system is presented of the nine fundamental morphological types. With the aid of a uniform system of graphs to represent the floral structures one can read the general character of the flower and even special details may be indicated as nectar spurs, appendages, etc. One can thus easily compare a phylogenetic series of flowers and the evolutionary progression is often shown in a striking manner. It is important that the same general graph always represents the same floral organ or structure and that the diagrams can be constructed easily with the aid of compass and pen.

#### THE NINE FUNDAMENTAL MORPHOLOGICAL FLOWER TYPES

1. Hypogynous flower. In this first and simplest type there is no special expansion or differential growth of the floral axis. The general morphological system and mode of development is the same as in the primitive flowers of *Equisetum*, *Lycopodium*, *Selaginella*, cycads, and coni-

<sup>3</sup> Schaffner, John H. A general system of floral diagrams. Ohio Jour. Sci. 16: 360-364. 1916.



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fers. Occasionally there is a slight enlargement of the floral axis, especially in the gynecium axis, as in the primitive *Araucaria Cookii* R. Br., but this is not taken into account unless the expansion is pronounced. Examples of the first flower type: *Echinodorus*, *Magnolia*, *Yucca*, *Tradescantia*, *Delphinium*, *Oxalis*, *Viola*, *Rhododendron*, *Catalpa*. Pl. 12, fig. 1. *Ranunculus abortivus* L. (Ranunculaceae).

2. Hypogynous flower with expanded gynecium axis. This type of flower is essentially the same as the primitive hypogynous type except that it has a hereditary potentiality which causes a decided expansion of the upper part of the floral axis which is in the secondary female state. Familiar examples are *Sagittaria latifolia* Willd. (carpellate flower) and pl. 12, fig. 2. *Nelumbo lutea* (Willd.) Pers. (Nelumbonaceae).

3. Perigynous flower with free hypogynous hypanthium and normal gynecium axis. This is the common perigynous type, all the floral organs except the carpels being borne on the perigynous disk or hypanthium. The hypanthium may vary from only a slight rim to a very prominent cup-like organ. Examples: *Rosa*, *Agrimonia*, *Lythrum*, *Amygdalus*, *Baptisia*, *Hamamelis*, *Ulmus*. Pl. 12, fig. 3. *Geum vernum* (Raf.) T. & G. (Rosaceae).

4. Perigynous flower with the entire floral axis expanded continuously. In this type the floral organs are borne on a broad cup-like disc and as the neutral transition zone between the gynecium and andrecium is about in the middle of the cup both staminodes and carpellodes may be present in a bisporangiate flower. This is apparently a rare type. Examples: *Meratia*, *Monimia*. Pl. 12, fig. 4. *Calycanthus floridus* L. (Calycanthaceae).

5. Perigynous flower with hypogynous hypanthium and separately expanded gynecium axis. In this flower type the transition zone of the floral axis in the neutral condition is not influenced by the expansion factors. Examples: *Duchesnea*, *Comarum*. Pl. 12, fig. 5. *Fragaria virginiana* Duchesne (Rosaceae).

6. Perigynous flower with adnate hypogynous hypanthium. Although this type of flower superficially resembles the ordinary epigynous type it is very different in its incipient stage, beginning its development much like an ordinary perigynous flower. In most cases also the plants with flowers of this type plainly show their relationship to typical perigynous groups, as for example the apple to the rose family. As development proceeds the neutral zone of tissue between the gynecium axis and the hypanthium also grows, thus producing a complete adnation except at the outer end where the short cup usually seen in apples represents the hypanthium developed in the incipient stage. Examples: *Pyrus*, *Amelanchier*, *Crataegus*, *Carya*, *Juglans*. Pl. 12, fig. 6. *Malus sylvestris* Mill. (Rosaceae).

7. Epigynous flower without hypanthium. In this flower type the morphological apex of the floral axis is in the base of the ovulary and

growth of the cortical tissues does not extend beyond the ovulary wall. It is a common and wide-spread type found in many groups. Examples: *Vallisneria*, *Hypoxis*, *Sisyrinchium*, *Canna*, *Cypripedium*, *Portulaca*, *Vaccinium*, *Opuntia*, *Philadelphus*, *Asarum*, *Pastinaca*, *Cornus*, *Lobelia*, *Helianthus*. Pl. 12, fig. 7. *Cynoxylon floridum* (L.) Raf. (Cornaceae).

8. Epigynous flower with tubular epigynous hypanthium. In this type the cortical tissue, as it passes into the secondary male state at the top of the ovulary, continues its growth and produces a tube of greater or less length at the end of which the sepals, petals, and stamens are borne. Examples: *Euryale*, *Crinum*, *Hymenocallis*, *Cereus*, *Epiphyllum*, *Ribes odoratum* Wendl., *Oenothera*. Pl. 12, fig. 8. *Fuchsia hybrida* Voss. (Onagraceae).

9. Epigynous flower with solid epigynous hypanthium. In this type the lower part of the hypanthium and the style, above the ovulary, develop as a continuous tissue. In most cases there is a tubular upper part of the hypanthium above the solid portion, which indicates that this type probably evolved from the tubular epigynous hypanthium. It is interesting to note that Dr. G. H. Shull obtained a mutant *Oenothera* with a solid epigynous hypanthium from the ordinary tubular epigynous hypanthium type. Examples: *Iris*, *Strelitzia* and Shull's mutant *Oenothera pollicata*. Pl. 12, fig. 9. *Iris cristata* Ait. (Iridaceae).

In some plants there is an elongation of the upper part of the ovulary, as it ripens, which simulates to some extent the solid epigynous hypanthium. Such a condition is present in *Taraxacum*, *Tragopogon*, *Lactuca virosa* L., etc., but as the structure is developed more especially in relation to the fruit rather than the flower it should not be associated with the ninth flower type. It will be noted that this elongation of the upper part of the fruit is found in plants which have the simple epigynous condition.

#### MORPHOLOGICAL DESCRIPTION OF THE FLOWERS WHOSE DIAGRAMS ARE REPRESENTED IN PLATE 13

An inspection of the diagrams will readily show the character of the signs used to represent the various floral organs and structural conditions. In general a star represents a missing member; a completely black or stippled sporophyll graph indicates that the organ is vestigial to a greater or less degree, either because of determination of the floral axis, or because of the inhibitory influence produced by a secondary sexual condition in a monosporangiate flower, or because of the neutral condition produced on a zone where sex reversal is taking place. Connecting lines indicate union of parts or organs situated on a structure. If the stamens are very numerous in a perigynous or epigynous flower the connecting lines to these may be omitted, since the connecting lines from the sepals

and petals will indicate their position in the flower. The hypanthium is represented by a broad dotted circle and the inferior ovulary is drawn with an extra heavy circle. Adnation between the ovulary and hypogynous hypanthium is indicated by stippling, and the solid epigynous hypanthium both by connecting lines and stippling. An expanded gynecium axis is represented by an ordinary circle around the carpels. Union of perianth segments of two cycles forming an ordinary perianth tube is indicated by connecting lines between the ends of the successive inner and outer segment graphs. In case of a prominent spiral arrangement, this character can be indicated by drawing one or more spiral lines to connect the proper members of the spiral. Bracts of an involucre or subtending bracts are represented by ordinary lines to distinguish them from sepals. The secondary axis on which the flower is borne is indicated by a small circle with a dot in the center. The relation of the primary axis to the secondary axis is sometimes not easy to determine and in such a case it should be omitted until the relationship is definitely known. If the anthers are bilocular (with two microsporangia) the horizontal line producing four divisions in the anther graph is omitted.

In present systematic descriptions the terminology used is both improper and confusing and cannot be depended upon for learning the actual condition. Thus the anthers of *Lilium* are said to be "2-celled" and those of *Smilax* are also described as "2-celled," but the first has four microsporangia while the second has two microsporangia in each anther.

All of the figures refer to plate 13.

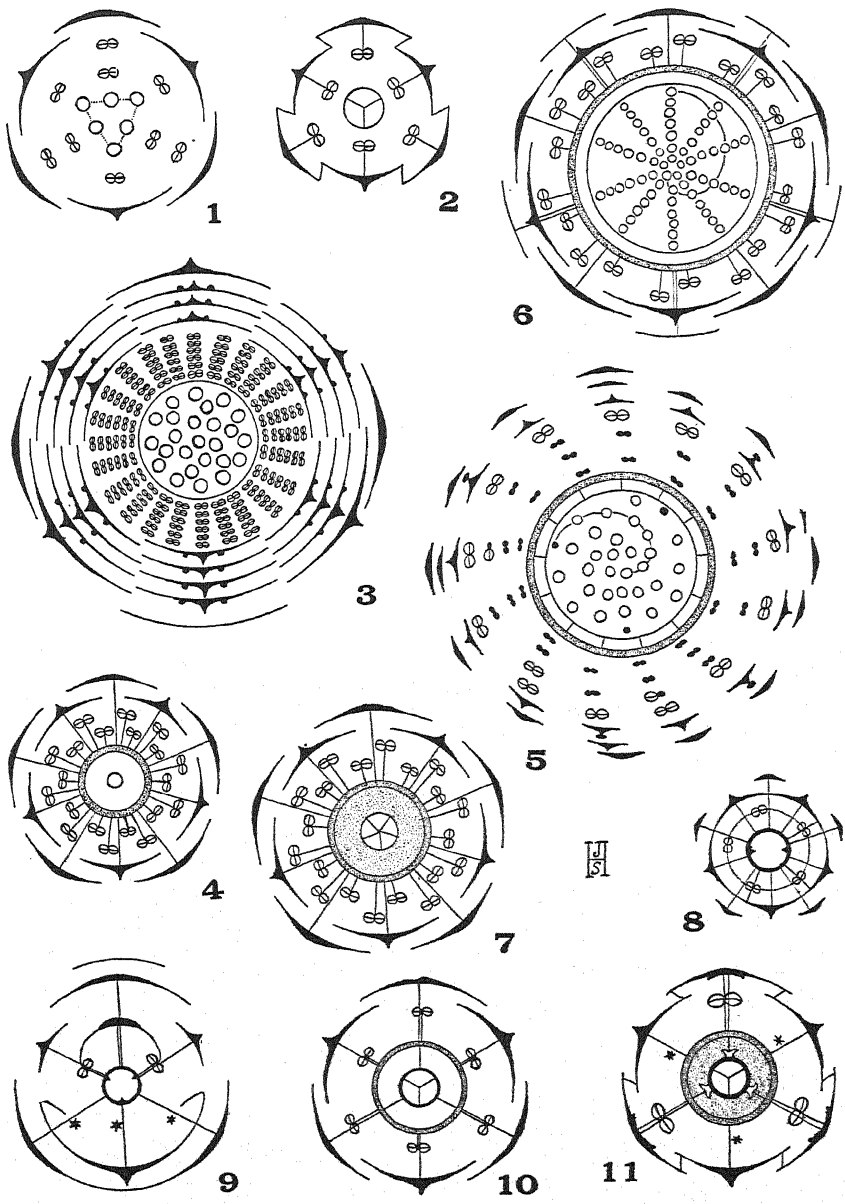
Fig. 1. *Butomus umbellatus* L. (Butomaceae). Flower hypogynous, bisporangiate, heptacyclic, trimerous, actinomorphic, choripetalous; carpels slightly united.

Fig. 2. *Polygonatum commutatum* (R. & S.) Dietr. (Liliaceae). Flower hypogynous, bisporangiate, pentacyclic, trimerous, actinomorphic; perianth segments (sepals and petals) united into a perianth tube; stamens united with the perianth; syncarpous, ovulary trilocular.

Fig. 3. *Nelumbo lutea* (Willd.) Pers. (Nelumbonaceae). Flower hypogynous, bisporangiate, choripetalous; calyx dimerous; corolla trimerous, with numerous petal-like staminodes; stamens and carpels free, in spirals, the carpels in a greatly expanded gynecium receptacle. The expansion of the receptacle is indicated by the circle surrounding the carpels.

Fig. 4. *Prunus virginiana* L. (Rosaceae). Flower perigynous with a free hypanthium, bisporangiate; perianth pentamerous, actinomorphic, choripetalous; carpel one.

Fig. 5. *Calycanthus floridus* L. (Calycanthaceae). Flower perigynous with a continuously expanded floral axis, bisporangiate, actinomorphic,



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the parts in spirals. The broad circle represents the expanded andrecium axis and the narrow inner one the expanded gynecium axis. The connecting lines between the two indicate that the two are continuous; on the neutral transition between the normal carpels and stamens are some staminodes and carpellodes represented in black.

Fig. 6. *Fragaria chiloensis* Duchesne. (Rosaceae). Flower perigynous with separately expanded gynecium axis and hypogynous hypanthium, bisporangiate, actinomorphic; perianth pentamerous, choripetalous, the calyx with five alternate bractlets; carpels spirally arranged; neutral zone of the floral axis not affected by the expansion potentialities.

Fig. 7. *Malus sylvestris* Mill. (Rosaceae). Flower perigynous with adnate hypogynous hypanthium, bisporangiate, actinomorphic, choripetalous, syncarpous, plurilocular; calyx, corolla, and gynecium pentamerous. The stippling between the hypanthium and the ovulary indicates adnation.

Fig. 8. *Sclerolepis uniflora* (Walt.) B. S. P. (Helianthaceae). Flower epigynous without hypanthium, bisporangiate, tetracyclic, pentamerous, actinomorphic, sympetalous; ovulary of two united carpels, unilocular; calyx (pappus) of five distinct sepals (scales); stamens synantherous, their filaments united with the corolla.

Fig. 9. *Cypripedium parviflorum* Salisb. (Orchidaceae). Flower epigynous without hypanthium, bisporangiate, pentacyclic, trimerous, choripetalous, zygomorphic; ovulary unilocular; two sepals united; lip petal large; the odd upper stamen represented by a large staminode and connected with the two fertile stamens with the style (column). The stars represent missing stamens.

Fig. 10. *Crinum asiaticum* L. (Amaryllidaceae). Flower epigynous with tubular epigynous hypanthium, bisporangiate, pentacyclic, trimerous, choripetalous, actinomorphic; ovulary trilocular. The lines connecting the hypanthium with the ovulary without stippling in between indicate an epigynous hypanthium.

Fig. 11. *Iris cristata* Ait. (Iridaceae). Flower epigynous with solid epigynous hypanthium, bisporangiate, pentacyclic with the inner cycle of stamens wanting, trimerous, actinomorphic; ovulary trilocular. The crests on the sepals are indicated and also the peculiar petal-like condition of the stigmas. The lines connecting the hypanthium with the ovulary and the stippling in between indicate a solid epigynous hypanthium. The connecting lines passing from the anthers to the perianth segments show that the stamens are united with the perianth.

## Further data on monosporous cultures of *Gelasinospora tetrasperma*

IRIS CAMPBELL<sup>1</sup>

WITH TWO FIGURES

Among Ascomycetes there occur here and there species characterized by having four-spored asci. Species of this kind that have been studied so far all belong to the type referred to as facultatively heterothallic. Each ascospore is normally provided with two nuclei of opposite sex at its origin. When one finds normal sized spores which prove to be unisexual it has been assumed that the mechanism for spore formation has in some way been interfered with so that two nuclei of the same sex are included in a spore.

Lindegren (1933) stated that in *Neurospora crassa* second division segregation of Mendelian factors represents crossing-over, and, therefore, second division segregation percentages can be used to compute chromosome map distances. He has recently (1936) suggested, however, that where there is more than a 67 per cent second division segregation the genes concerned are too far apart to work with. Colson (1934) had suggested that since the spindles of the second division in the ascus of *Neurospora tetrasperma* are oriented more or less parallel as in conjugate division, spores with two nuclei of the same sex would be cut out provided the sex factors segregated in the second division and the two nuclei of the same sex moved in the same direction. Kniep (1929) and Lindegren (1932) had previously figured such a condition. Therefore, according to Colson's interpretation, when one finds in such forms as *Neurospora tetrasperma* normal sized unisexual spores, the percentage of such spores ought to represent the actual percentage of crossing-over. None of the authors referred to above has considered the type of spindle orientation, reported by Dodge (1927, 1937) to be not only very common in *Neurospora tetrasperma*, but regular at second division in *Gelasinospora tetrasperma*, where one spindle is placed well above the other (fig. 1). No one has heretofore suggested that normal sized unisexual spores in these facultatively heterothallic species could arise as a result of degeneration of one or more nuclei in the ascus previous to spore delimitation.

Judging from Dodge's (1937) cytological work on *Gelasinospora tetrasperma*, it might very well be that the two undivided nuclei which are shown in his figures 18 and 22 would have degenerated later without

<sup>1</sup> Paper read at a meeting of the Mycological Society of America held at Atlantic City Dec. 30, 1936. This work was done with the aid of scholarships given by The New York Botanical Garden.

undergoing division, as frequently happens in Ascomycetes. Dodge suggested that the ascus shown in his figure 18 may have been abnormal, and that the two upper nuclei in that ascus may have been degenerating.

Miss Seaver (1937) has suggested another way by which normal sized ascospores might prove to be unisexual when germinated. In our culture work with *Neurospora* and *Gelasinospora* we have employed the heat treatment method to induce germination. Miss Seaver found that she had a larger percentage of unisexual spores that were sex *a* than those

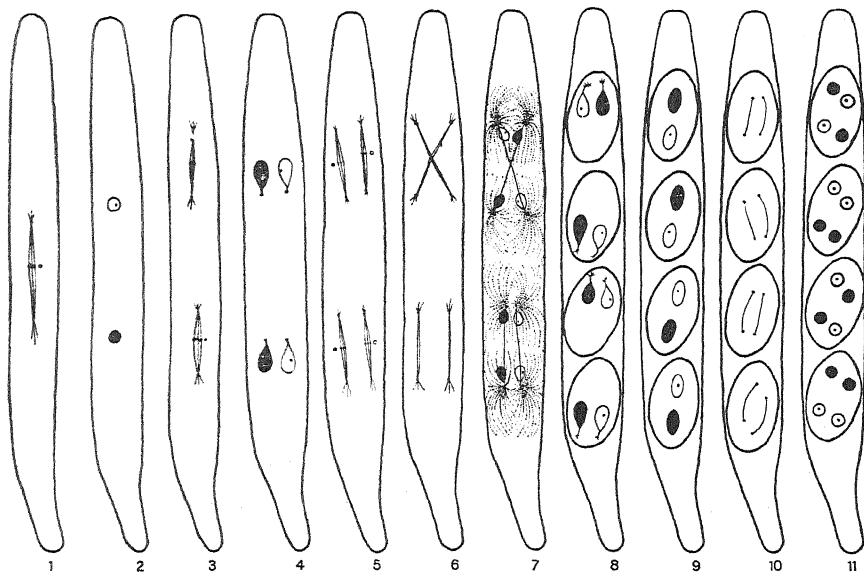


Fig. 1. Diagram showing spindle orientation and mechanics of spore delimitation in a normal ascus of *Gelasinospora tetrasperma*. The four nuclei following second division are pear-shaped and they are arranged in pairs, two at one end and two at the opposite end of the ascus. The four spindles of the third division are also arranged in pairs. The spindles of a pair may be either crossed or parallel. These third divisions spindles persist until spore delimitation is well along, certainly a very efficient mechanism for insuring the inclusion of the nuclei of opposite sex in each normal spore. Adapted from Dodge (1937).

that were of sex *A*. It occurred to her that the heat treatment either killed the nuclei of one sex or delayed their divisions. In this case the uninjured nuclei would divide rapidly and thus pervade the entire mycelium. It might be that the nuclei that were merely injured would later divide a few times. This would account for long delayed ascocarp formation which was very common in our *Gelasinospora* cultures. Some cultures produced perithecia only after several weeks. The stock from which the ascospores

were obtained had been stored in a refrigerator for several months. Both of these explanations would seem to be plausible from my own work on *Gelasinospora*, although, as will be noted later, the nuclei of one sex appear to be no more susceptible to injury than those of the other sex.

In *Gelasinospora tetrasperma* as stated previously the spindles of the second division are always placed one above the other, rather widely separated. If the sex attraction should frequently prove not strong enough to bring about reorientation of the resulting four nuclei through nuclear migrations this would often be reflected in the delimitation of unisexual spores or of spores containing two nuclei of the same sex.

Of 650 cultures obtained from normal sized spores 38 proved to be unisexual. The two sexes were equally represented. Upon measuring the spores it was found that 36 were normal in size, the other two were dwarfs. Dowding found that only one spore in two thousand from a spore print was of the dwarf type. On the basis of such a small percentage it would not seem to be absolutely necessary to measure the spores that proved to be unisexual, though this was done in our experiment. Dowding germinated about 150 normal sized ascospores of *Pleurage anserina* and found them all to be bisexual, whereas in her *Gelasinospora*, of the 26 normal sized and ten giant spores only one, which happened to be a giant spore, proved to be unisexual. Her experiments were carried out by allowing these ascospores to germinate without heat treatment. It would seem that with the culture medium she used spores sometimes germinate without heating. She later found that heat treatment increased the percentage of germination about three times. In our experiments using cornmeal agar we had little success in obtaining germination without heating.

Since *G. tetrasperma* has very few striking mycelial characteristics which could be used in genetic work it would be difficult to analyze the nuclear complement of these normal sized unisexual spores. In *Neurospora tetrasperma*, however, conidia are produced by normal races of both sexes, but more abundantly by the mycelia of one sex (sex *a*) than by the other (sex *A*). Through interspecific crosses and x-ray treatment, Dodge has developed non-conidial as well as lethal races. With such material one could prove definitely whether normal sized unisexual spores actually contained two nuclei of the same sex at their origin. It would seem from preliminary work that frequently they may not. On this basis one could account for their unisexual condition by assuming either injury to the nuclei of one sex by heat treatment, or by a nuclear degeneration preceding spore formation. The size of an ascospore is often determined by the amount of competition existing between the spores actually cut out. With degeneration of two of the four nuclei resulting from the second



division, the third division occurring normally for the other two, four uninucleate spores would be delimited and these would naturally be about as large as if they had two nuclei at their origin. But having only one nucleus each they must be unisexual.

The mechanism for insuring that each ascospore has two nuclei of opposite sex at its origin is much more nearly perfect in *Gelasinospora tetrasperma* than it is in *Neurospora tetrasperma*. Therefore, it would seem logical to assume that when normal sized spores are proved beyond doubt to be unisexual, one or more of the ascus nuclei must have degenerated before spore formation. This point should be fully considered in all genetic work dealing with these facultatively heterothallic Ascomycetes.

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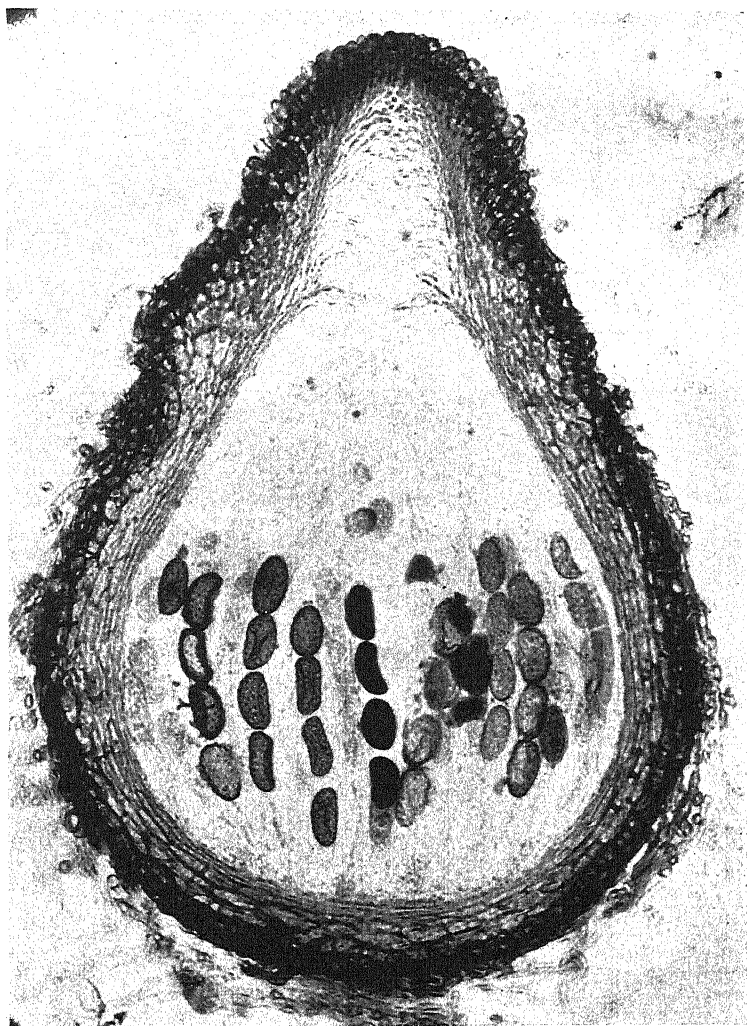


Fig. 2. Section of mature perithecium of *Gelasinospora tetrasperma* showing the characteristically "pitted" spores.



## Razumovia Sprengel versus Centranthera R. Brown

E. D. MERRILL

In 1901 James Britten<sup>1</sup> published the following note on this case, which seems rather generally to have been overlooked until 1931 when Alston<sup>2</sup> accepted his manifestly correct conclusions and published two additional binomials under *Razumovia*.

"This genus [*Razumovia*] was founded by Sprengel in 1807 (Mant. Prima, 1807, p. 45) for the plant subsequently known as *Centranthera humifusa* Wall., a name retained in the *Flora of British India* (iv. 301), where, however, Sprengel's name is cited as a synonym. *Razumovia* clearly antedates *Centranthera*, which was published by Brown (Prodr. 438) in 1810. *C. hispida* Br. will therefore stand as *RAZUMOVIA HISPIDA* and *C. humifusa* will be superseded by *R. TRANQUEBARICA* Spreng."

This is an absolutely clear case of priority, and no valid reason appears why Britten and Alston should not be followed. The genus is a small one, with no species of economic or of horticultural importance. Moreover a change of generic name for this small scrophulariaceous genus is desirable to avoid possible confusion with the very similar *Centratherum* Cassini (1817), a distinctly larger and more widely distributed genus of the Compositae, and *Centranthus* de Candolle (1805), a somewhat larger genus of the Valerianaceae. The use of *Razumovia* Sprengel in Juss. Dict. Sci. Nat. 44: 526. 1826, with its type species *R. paniculata* Spreng. listed in DC. Prodr. 6: 158. 1837 as a synonym of *Humea elegans* Smith, has no bearing on the case as it is a later generic homonym, and is a synonym of the much earlier *Humea elegans* Smith, Exot. Bot. 1: t.1. 1804, of the Compositae. *Purshia* Dennst. Schluss. Hort. Malabar. 35. 1818, is not validly published for no generic description was given. Dennstaedt merely published the binomial *Purshia ciliata* with a reference to *Corosinam* Rheede, Hort. Malabar. 9: 133. t. 68. 1689, thus: "68. Corosinam—*Purshia ciliata*. Mihi." Dillwyn, Rev. Ref. Hort. Malabar. 47, 1839, with expressed doubt, thought that *Centranthera hispida* might be represented but I believe that Rheede's crude illustration belongs with *Razumovia indica* (Linn.) Alston. In any case, as a generic name, *Purshia* Dennst. is invalidated by *Purshia* DC. which is one year earlier, while *Razumovia* Sprengel has eight years priority. *Gumteolis* Ham. in D. Don Prodr. Fl. Nepal 87. 1825 was merely published in synonymy, without a binomial. There is but a single excluded binomial, *Centranthera prostrata* Boj. = *Radamaea prostrata* Benth.

<sup>1</sup> Britten, J. Jour. Bot. 39: 69. 1901.

<sup>2</sup> Alston, A. H. G. in Trimen, H. A hand-book of the flora of Ceylon 6: (Suppl.) 217. 1931.

In connection with this study I am under obligations to the authorities of the Rijks Herbarium, Leiden, the Royal Botanic Gardens, Kew, the New York Botanical Garden, and the United States National Herbarium for the loan of important study material, to Dr. G. Taylor of the British Museum for a note on authentic material representing the true *Centranthera hispida* R. Br., and to Mr. C. T. White of Brisbane, and R. H. Anderson of Sydney, for Australian material.

## KEY TO THE RECOGNIZED SPECIES

1. Leaves broad, longitudinally 3-nerved, sparingly toothed; flowers large, about 5 cm. long, bracts broad. .... 1. *R. grandiflora*.
1. Leaves narrow, entire, not longitudinally nerved.
  2. Vegetative parts more or less hispid, hirsute, or lepidote.
    3. Calyx inflated, 2 cm. long. .... 2. *R. Hookeri*.
    3. Calyx much smaller, rarely 1.3 cm. long.
      4. Coarse, erect, simple or branched, hispid or hirsute plants, the flowers 1.5 to 4 cm. long.
        5. Calyx 3-toothed, 3-winged. .... 3. *R. Chevalieri*.
        5. Calyx not toothed or winged.
          6. Calyx with few to many elongated, stiff, spreading hairs, the indumentum on the vegetative parts similar in type.
            7. Corolla 3 to 3.5 cm. long. .... 4. *R. Brunonian*.
            7. Corolla 2 to 2.5 cm. long. .... 5. *R. indica*.
          6. Calyx rather densely appressed-hirsute, the vegetative parts hispid.
            7. Corolla 3 to 4 cm. long. .... 6. *C. longiflora*.
            7. Corolla 1.5 to 2.5 cm. long.
              8. Corolla mostly yellow, 1.5 to 2 cm. long. .... 7. *C. cochinchinensis*.
              8. Corolla mostly pink-purple, 1.5 cm. long. .... 7a. var. *nepalensis*.
              8. Corolla yellow or yellow inside and pink-purple outside, sometimes pink or purple, 2.5 cm. long. .... 7b. var. *hispida*.
          4. Small prostrate plants, the flowers less than 1 cm. long, leaves linear, more or less lepidote, the upper ones alternate. .... 8. *R. tranquebarica*.
      2. Vegetative parts glabrous or nearly so, flowers 1 to 1.2 cm. long, all leaves opposite. .... 9. *R. tonkinensis*.

1. *Razumovia grandiflora* (Benth.) comb. nov.

*Centranthera grandiflora* Benth. in Wall. List no. 3880. 1830, *nomen nudum*, Scroph. Ind. 50. 1835, DC. Prodr. 10: 525. 1846; Hook. f. Fl. Brit. Ind. 4: 301. 1884; Prain, Jour. As. Soc. Bengal 72(2): 21. 1903; Bonati in Lecomte Fl. Gén. Indo-Chine 4: 449. 1927.

*Centranthera maxima* Bonati, Bull. Soc. Bot. Genève II 5: 140. 1913.

A characteristic species extending from Assam, Khasia, and the Sikkim Himalayan region to Burma, Indochina and southern China. Specimens examined: Sikkim, *Hooker*, Khasia, *Hooker & Thomson* (5 sheets); Shillong, alt. 6000 ft., *C. B. Clarke* 38476, Tserra Rin, 4500 ft., *C. B. Clarke* 7190 (=5174); eastern Bengal, *Griffith* 39361; Assam and Khasia, Tea Deputation ex Herb. Calcutta: China, Kweichow Province near Sohu, *Y. Tsiang*

7348, on open slopes, flowers yellow, Sept. 27, 1930; Kwangsi Province, Bako Shan near the Yunnan border, *R. C. Ching* 7363, Sept. 12, 1928, on open slopes, altitude about 700 m., flowers lemon yellow.

2. *Razumovia Hookeri* sp. nov.

Species *R. grandiflorae* (Benth.) Merr. affinis, differt foliis multo angustioribus, 2–5 mm. latis, integerrimis, 1-nerviis haud longitudinaliter 3-nerviis. Herba erecta, ramosa, plus minusve asperula, saltem 45 cm. alta; ramis consperse breviter hispidulis; foliis lineari-lanceolatis vel anguste lanceolatis, integerrimis, 2.5–6 cm. longis, 3–5 mm. latis, obtusis acutis vel obscure acumina-tis, sessilibus vel brevissime petiolatis, supra hispidulo-asperulis, margine revolutis, subtus consperse hispidulis; floribus in axillis superioribus, sessilibus, saltem 2.5 cm. longis, calycibus spathaceis, ovoideis vel oblongo-ovoideis, acuminatis, circiter 2 cm. longis, longitudinaliter circiter 8-carinatis, carinae hispidulae; corolla paullo exserta (immatura), deorsum angustata et consperse hispidula.

India, Sikkim, tropical regions, altitude 3000–4000 feet, *J. D. Hooker* (type), herb. Gray, isotype herb. Lugd.-Bat.

This collection was distributed from Kew as representing *Centranthera grandiflora* Benth., and while the proposed new species is manifestly allied to the latter it differs radically in its very narrow, entire leaves which present no indications of the rather conspicuous lateral longitudinal nerves so evident in *Razumovia grandiflora* (Benth.) Merr. It is suspected that mature flowers may be considerably larger than indicated in the description, probably approximating those of *R. grandiflora*, whose corollas attain a length of about 5 cm. There are no fully mature flowers on the two sheets examined. In typical *R. grandiflora* (Benth.) Merr., the leaves are very much broader, always conspicuously longitudinally 3-nerved, even the smaller leaves on the ultimate branches, while they are also usually dis-tantly toothed.

3. *Razumovia Chevalieri* (Bonati) comb. nov.

*Centranthera Chevalieri* Bonati, Bull. Soc. Bot. France 71: 1099. 1924, Lecomte, Fl. Gén. Indo-Chine 4: 448. f. 46, 15, 47, 7–8. 1927.

Indochina, Annam, Nhatrang, *Chevalier* 30466, type collection, not seen.

Judging from the description this species should be allied to *Centran-thera Brunoniana* (Wall.) Merr., but it has much smaller flowers than the latter species.

4. *Razumovia Brunoniana* (Wall.) comb. nov.

*Centranthera Brunoniana* Wall. List no. 3882. 1830, *nomen nudum*; Benth.

Scroph. Ind. 50. 1835, DC. Prodr. 10: 525. 1846; Hook. f. Fl. Brit. Ind. 4: 301. 1884; ? Bonati in Lecomte, Fl. Gén. Indo-Chine 4: 449. 1927.  
*Centranthera procumbens* Benth. var. *latifolia* O. Ktz. Rev. Gen. Pl. 459. 1891.

The type of this species is *Wallich* 3882 from Moulmein, and it is, of course, possible that more than one species was included under this number. In Bentham's original description of 1835 he merely says "Moolmyne, Wallich"; in his second description of 1846 "In Martabania (Wallich!)." The specimen of this number that I have seen, herb. Kew, is the Moulmein sheet from Bentham's own herbarium and I suspect that this is the one on which the first published description was based. It is very closely matched by *Lobb* 359 bis, herb. Kew, and *Kuntze* 6223 (type of *C. procumbens* Benth. var. *latifolia* O. Ktz.), herb. New York, both from Moulmein. Its alliance is definitely with *Razumovia indica* (Linn.) Alston, and it is distinguishable from the latter species only by certain minor characters. From the not very ample original descriptions it has by some authors been considered nearer *Centranthera hispida* R. Br. While Bonati credits this species to Indochina, yet one suspects that he had long-flowered forms of *Centranthera hispida* R. Br. However, the species has been recorded from Siam, and one might reasonably expect that it extends to Indochina. Hooker f. (Fl. Brit. Ind. 4: 301. 1884), credits it to China on the basis of Bentham's description of the yellow-flowered form (*Centranthera hispida* R. Br.; Benth. Fl. Hongk. 254. 1861) but Bentham himself (Hook. Jour. Bot. 5: 131. 1853) under "var. floribus pallide flavis" states that he could find no distinctive characters, other than the flower color, and notes that the color is known to vary in other hemiparasitic species of Scrophulariaceae. Hance (Jour. Bot. 23: 326. 1885) referred a Kwangtung specimen to *C. Brunoniana* Wall., making his identification wholly from Bentham's descriptions. Hemsley (Jour. Linn. Soc. Bot. 26: 201. 1890) admitted the species as a Chinese one but made this significant statement: "We have referred the yellow flowered specimens to *C. Brunoniana*, Wall., and the purple ones to *C. hispida* R. Br., without any confidence of their distinctness." *Razumovia Brunoniana* (Wall.) Merr. seems to be confined to Tenasserim, Burma, Siam, and perhaps Indochina. I have seen no specimens from China that can be referred to it. The Chinese and Japanese forms that have been identified as representing *Centranthera Brunoniana* Wall., are referable, I believe, to *Razumovia cochinchinensis* (Lour.) Merr.

5. *Razumovia indica* (Linn.) Alston in Trimen, Fl. Ceyl. 6: (Suppl.) 217. 1931.

*Rhinanthus indica* Linn. Sp. Pl. 603. 1753; Trimen, Jour. Linn. Soc. Bot. 24: 145. 1887.

*Purshia ciliata* Dennst. Schluss. Hort. Malabra. 35. 1818.

*Centranthera procumbens* Benth. in DC. Prodr. 10: 525. 1846; Hook. f. Fl. Brit. Ind. 4: 301. 1884; Trimen, Fl. Ceyl. 3: 259. t. 68. 1895; Petch, Ann. Bot. Gard. Peradeniya 6: 69. 1915.

*Centranthera indica* Gamble, Fl. Madras 971. 1924.

*Centranthera Brunoniana* sensu Thwaites, Enum. Pl. Zeyl. 220. 1864, non Benth.

*Corosinam* Rheede, Hort. Malabar. 9: 133. t. 68. 1689.

This species is well illustrated by Trimen, occurring in India, the Deccan Peninsula, Concan (*Stocks!*), and southward, and in Ceylon (*Thwaites 2026!*) The Linnaean species was essentially based on *Rhinanthus foliis lanceolatis* Linn. Fl. Zeyl. 107. 1747, and I interpret the species by this reference. *Hyssopus zeylanicus tenellus pratensis* Burm. Thes. Zeyl. 122. 1737 is also cited as a synonym, but is not the same as the Flora Zeylanica specimen. Hermann's Ceylon specimen, the basis of the original Linnean description of the Flora Zeylanica is *Centranthera procumbens* Benth. as confirmed by Trimen, Jour. Linn. Soc. Bot. 24: 145. 1887. Trimen calls attention to the fact that Hooker f. reduced the Linnaean species to the very different *Geniosporum elongatum* Benth.; but this reduction, from Hooker's citation, was manifestly based on the Burman Thesaurus reference and on the younger Burman's misinterpretation of *Rhinanthus indica* Linn., Fl. Ind. 131. t. 39 f. 1. 1768. The two Burman references involved apparently appertain to *Geniosporum tenuiflorum* (Linn.) Merr. In the synonymy, as given above, *Centranthera indica* Gamble was published without reference to its name-bringing synonym, Gamble merely citing *Centranthera procumbens* Benth. with reference to Hooker's and Trimen's treatments of it. *Purshia ciliata* Dennst. is an invalid binomial, as Dennstaedt did not publish a description of his genus *Purshia*, merely stating that *Corosinam* Rheede was *Purshia ciliata* Dennst.

#### 6. *Razumovia longiflora* sp. nov.

Species *R. cochinchinensis* (Lour.) Merr. simillimis et affinis, differt floribus multo longioribus, 3.5–4 cm. longis. Herba perennis, erecta, hispida, simplex vel ramosa, 30–60 cm. alta; foliis anguste oblongis vel sub lanceolatis, 2–3 cm. longis superioribus multo brevioribus, 3–5 mm. latis, utrinque hispidulis, obtusis vel acuminatis, nervis lateralibus obsoletis; floribus sessilibus, calycibus spathaceis, acuminatis, circiter 1.3 cm. longis, extus subdense adpresse hispidis, intus glabris vel consperse breviter hirsutis, obscure longitudinaliter nervosis, bracteis quam calycibus multo brevioribus, rigidis, hispidis, anguste oblongis vel lanceolato-ovatis, 4–6 mm. longis; corolla subglabra vel extus



conspersa pubescens, 3.5–4 cm. longa, tubo deorsum angustato; capsula glabra, circiter 1 cm. longa.

China, Kwangtung Province, Taai Yeung Shan, *F. A. McClure* 7241, July 18, 1921, on dry grassy slopes, altitude 600 m., flowers white with red and yellow markings. Indochina, Annam, Quang Binh Province, My Duc, *A. Petelot* 4189, July, 1930, herb. N. Y. Bot. Gard. (type). It is suspected that *McClure* 6534 from Taai Yeung Shan, Kwangtung Province, is also referable here, but the specimen is a very poor and incomplete one.

With an extreme interpretation of *Razumovia cochinchinensis* (Lour.) Merr. as having flowers 1.5 to 4 cm. long, this form might be placed there because of its habit, indumentum, and other characters. I have hesitated in placing under the latter species specimens that vary from 1.5 to 2.5 cm. in flower length, and prefer to characterize this long flowered form as a distinct species. It would not be surprising if some of the Indochina material that Bonati referred to *Centranthera Brunoniana* Wall. actually appertained to this species, rather than to Wallich's species or to *R. cochinchinensis* (Lour.) Merr. (*Centranthera hispida* R. Br.). The chief character by which this proposed new species may be distinguished from *Centranthera cochinchinensis* (Lour.) Merr. is by its unusually long flowers, the corollas being from 3.5 to 4 cm. in length. A form of this species may have been the basis of some of the Chinese records of *Centranthera Brunoniana* Wall.

7. *Razumovia cochinchinensis* (Lour.) comb. nov.

*Digitalis cochinchinensis* Lour. Fl. Cochinch. 378. 1790, ed. 2, 459. 1793.

*Centranthera hispida* sensu Benth. in Hook. Jour. Bot. 5: 131. 1853, Fl. Hongk. 254. 1861; Miq. Fl. Ind. Bot. 2: 707. 1857; Hemsl. Jour. Linn. Soc. Bot. 26: 202. 1890; Merr. Fl. Manila 421. 1912, Enum. Philip. Fl. Pl. 3: 442. 1893; Koord. Exkursionsfl. Java 3: 181. 1912; Bonati in Le-comte, Fl. Gén. Indo-Chine 4: 448. 1827, vix R. Brown.

*Centranthera Brunoniana* sensu Hemsl. Jour. Linn. Soc. Bot. 26: 201. 1890; Makino, Phan. Pterid. Jap. Ic. 1: t. 3. 1899, non Wall.

*Centranthera cochinchinensis* Merr. Trans. Am. Philos. Soc. II 24(2): 353. 1935.

Siam, *Hosseus* 196, *Kerr* 826; Indochina, *Petelot* 985, *Geoffrey* 493, *Robinson* 1075; China, Yunnan, *Henry* 12430, flowers pinkish or red; Kiangsi, *Tsiang* 9898, 10396, *Allison* 3, all with yellow flowers; Kweichow, *Tsiang* 7297, yellow; Hupeh, *Sun* 750, yellow, *Henry* 2245, 144 p.p.; Anhwei, *Ching* 9029; Kwangtung, *Liang* 61223, scarlet and yellow, *Lau* 2331, yellow; Hainan, *Tsang* 10228, *Liang* 62078, both yellow. Japan,

*Keiske, s.n.*, 530, Satsuma Province, *Masamume*; Tsoa and Sagaimi, collectors not given; Nagasaki, *Maximowicz* in 1863; Formosa, *Yamamoto* 1159; Philippines, Batan, *Penix* 3746, *Ramos* 80196, yellow; Camiguin *Edaño* 79216, yellow; Luzon, Cagayan, *Cuming* 1281, *Ramos* 27529; Zambales, *Ramos and Edaño* 44606; Pangasinan, *Ramos* 4872; Rizal, *Loher* 4361, *Merrill* 7430, fl. yellow, tube tinged with reddish purple; Benguet, *Williams* 943, yellow; Mindanao, Davao, *Copeland* 438; Sumatra, Toba, *Ouweschond* 263; Java, *Docters van Leeuwen* 49, *Backer* 8431, fl. yellow, tube partly red, 30334, herb. *Blume* 48, *Baumée* 808, fl. yellow, *Wisse* 93, fl. dirty yellow, *Lörzing* 2454, fl. yellow, *DeVriese & Teysmann*, *Junghuhn* 183, 583, fl. "roseus," Battalade. "fl. lutei"; Madoera, *Zollinger* 1188, "cor. lutea, extus fuscescens," *Backer* 20205, 20054, fl. yellow, tube purplish inside, *H. B.* 1736 (no collector).

If my interpretation of Loureiro's description be correct, as I believe it to be, his specific name is the oldest one for the collective species under consideration. His type was from Indochina, probably from the vicinity of Hue in Annam. He does not give the flower size but indicates its color as "albo-violaceus." His description is a very excellent one for the form above considered except in his statement that the calyx was 5-fid; for in *Razumovia* (*Centranthera*) the calyces are spathaceous. Here Loureiro apparently copied the calyx description from the generic characters of the genus in which he erroneously placed his species to make his species description conform to the characters of *Digitalis*. For the most part the corollas are yellow, sometimes yellow inside, the tube outside somewhat purplish or pinkish, occasionally the entire flower being reddish, pinkish, or purplish. The corollas vary from 1.5 to 2 cm. in length, rarely longer.

7a. *Razumovia cochinchinensis* (Lour.) Merr. var. *nepalensis* (D. Don) comb. nov.

*Centranthera nepalensis* D. Don, Prodr. Fl. Nepal. 88. 1825.

*Capraria rigida* Ham. in Wall. List no. 3881. 1830, in syn.

*Digitalis stricta* Roxb. Hort. Beng. 45. 1814, *nomen nudum*, Fl. Ind. ed. 2, 3: 99. 1832.

*Centranthera hispida* sensu Wall. Pl. As. Rar. 1: 39. t. 45. 1830; Benth. Scroph. Ind. 50. 1835; Wight, Illus. Ind. Bot. 2: 194. t. 165b. 1850; Griff. Notul. Pl. As. 4: 194. 1854; Dalz. & Gibs. Bombay Fl. 182. 1861; Hook. f. Fl. Brit. Ind. 4: 301. 1884, pro majore parte; Trimen, Fl. Ceyl. 3: 259. 1895; Nairne, Fl. Pl. West. India 220. 1894; Woodr. Jour. Bombay Nat. Hist. Soc. 12: 175. 1898; Collet, Fl. Siml. 359. 1902; Prain, Bengal Pl. 776. 1903; Cooke, Fl. Presid. Bombay 2: 308. 1905; Duthie, Fl. Upper Ganget. Plain 2: 158. 1911; Haines, Fl. Bihar Orissa 637. 1922; Gamble, Fl. Presid. Madras 2: 971. 1924, vix R. Brown.

Nepal, *Wallich* 3881 (4 sheets); Kashmir, *Gammie*; Kumaon, *Strachey* & *Winterbottom*; Chota Nagpur, *Clarke* 21003a; Western Himalayan region, *Duthie* 18660; Bihar, *Duthie*; Mysore, collector not indicated; Upper Gangetic Plain, *Thomson*; Assam and Khasia hills, *Masters*; Ceylon, *Thwaites* 2025, *Macrae*; Eastern Tibet and southwestern China, *Forrest* 25109; Yunnan, *Delavay* 4824; Hupeh, *Henry* 140 p.p. (sheet 800,025 U. S. Nat. Herb.).

This form seems to differ consistently from *Razumovia cochinchinensis* (Lour.) Merr. in its somewhat smaller flowers, relatively somewhat broader corolla tubes, and usually purplish flowers, the corollas at most 1.5 cm. long. It is the form actually described by Bentham, Scroph. Ind. 50. 1835, from Indian material as *Centranthera hispida* R. Br. as having corollas 7 to 8 lines long, the same measurement being repeated in the Prodrusus description eleven years later. Yet the Australian form, and R. Brown's original description was based on an Australian specimen, has flowers about 2.5 cm. long, and Bentham himself noted this in his Flora Australiensis description in 1869. Wallich and Wight illustrate the flowers as pinkish-purple; Prain says "purplish"; Nairne "purplish red to nearly white"; Collet "pale purple or white"; Dalzell & Gibson "purplish red"; Duthie "purplish or white"; Cooke "rose-coloured or white"; Trimen "pink, tube orange yellow"; Haines "purple"; and Roxburgh "purple red."

7b. *Razumovia cochinchinensis* (Lour.) Merr. var. *hispida* (R. Br.) comb. nov.

*Centranthera hispida* R. Br. Prodr. 438. 1810; Benth. in DC. Prodr. 10: 925. 1846 quoad pl. Austr., Fl. Austral. 4: 513. 1869; F. M. Bailey, Syn. Queensl. Fl. 360. 1883, Queensl. Fl. 4: 1122. 1901; Moore & Betche, Handb. Fl. N.S.W. 342. 1893; Ewart & Davies, Fl. Northern Terr. 247. 1917, vix aliorum.

*Raxumovia hispida* Britten, Jour. Bot. 39: 69. 1901.

Australia, Roehampton Bay, ex herb. *Von Mueller* in 1868; Victoria River, ex herb. *Von Mueller*; Queensland, Proserpine and Kelsey Creek, *Michael* 853; Brisbane River, no collector indicated; Wide Bay, opposite Fraser Island, *Kajewski* 40, "flowers pink"; Stradbroke Island, *White*, s. n., "flowers purplish"; Walsh, *Barklay-Millar*, s. n. March, 1891; New Italy, Richmond River, *Bauerlen*; British New Guinea, *Brass* 3574, 5703, "flowers yellow."

*Centranthera hispida* R. Br. was described from Australian material collected by Banks in eastern tropical Australia, probably from the vicinity of the Endeavour River or the Bay of Inlets. The original specimen

seems to have been lost or misplaced, as Dr. G. Taylor informs me that the representative in the herbarium of the British Museum is a fruiting specimen labelled as having been in the Pallas Herbarium. This is doubtless a duplicate of the original collection, sent by Banks to Pallas and later returned to the Banksian Herbarium. Brown described the flowers as purplish but did not indicate their size. Various modern Australian collections have flowers about 2.5 cm. long (one inch), while the Australian botanists (Bentham, F. M. Bailey, Moore & Betche) indicate them as being "pink, purple, or yellow" or "pink outside and yellowish inside," and  $\frac{3}{4}$  to 1 inch long. Mr. C. T. White informs me that as he has observed the species the flowers are always purplish. In Australian flowering specimens that I have examined the flowers are about 2.5 cm. long. Boorman's color note on a specimen collected at Boonoo Boonoo, N. S. W., is yellow.

My attention was first directed to this study by the rather striking discrepancies noted in the descriptions based on Australian and on Indian specimens, these discrepancies involving particularly the size of the flower. I have frankly interpreted the species, under its oldest specific name, as a collective one. With more abundant and better material, for many of the specimens cited under *Razumovia cochinchinensis* and its varieties are in fruit, it may eventually be possible to characterize local microspecies in this group.

8. *Razumovia tranquebarica* Spreng. Fl. Hal. Mant. 45. 1807; Britten, Jour. Bot. 39: 69. 1901.

*Torenia lepidota* Roth, Nov. Pl. Sp. 281. 1821.

*Centranthera humifusa* Wall. List no. 3883. 1830, *nomen nudum*; Benth. Scroph. Ind. 50. 1835, DC. Prodr. 10: 535. 1846; Hook. f. Fl. Brit. Ind. 4: 301. 1884; Trimen, Fl. Ceyl. 3: 259. 1895; Prain, Bengal Pl. 776. 1903, Jour. As. Soc. Bengal 74(2): 364. 1905 (King, Mater. Fl. Malay. Penin. 4: 574); Haines, Fl. Bihar Orissa 4: 638. 1922; Ridl. Fl. Malay Penin. 2: 487. 1923; Gamble, Fl. Presid. Madras 2: 972. 1924; Bonati in Lecomte, Fl. Gén. Indo-Chine 4: 447. 1927.

*Cararia humifusa* Ham. in Wall. l.c. in syn.

*Razumovia lepidota* Alston in Trimen, Fl. Ceyl. 6: (Suppl.) 217. 1931.

This species is rather widely distributed in India and Ceylon extending to southeastern China, Malay Peninsula, Sumatra, Java, Borneo and Celebes. Specimens examined include the following: India, *Wight* 2216; Burma or the Malay Peninsula, *Griffith* 3937; Indochina, *Thorel* 375; Sumatra, *Rahmat Si Toroes* 3717; Java, *Backer* 19657, 20179; Borneo, Kudat and Jessleton, *Clemens* 9580, 9555; Celebes, Makassar, *Zollinger* 3292, Bonto Parang, *Beumée* 10672; Kangean Archipelago, *Backer*

27721; China, Hainan, *Liang* 62833; Kwangtung, *To Kang Peng* 12870, *Tso* 22189; Fukien, *Hance* 1461, *Chung* 6129, 6138.

9. *Razumovia tonkinensis* (Bonati) comb. nov.

*Centranthera tonkinensis* Bonati, Not. Syst. 1: 337. 1911, Lecomte, Fl. Gén. Indo-Chine 4: 447. 1927.

A species known only from Indochina, based on specimens collected by *Talmy* at Saigon, and *Balansa* 970 from Ouonbi, Tonkin. *Centranthera tonkinensis* Bonati var. *fastigiata* Bonati l.c. is described as a taller, much branched plant with elongated flexuose fastigiate branches; it was based on a *Thorel* specimen from Cochinchina. The species is apparently allied to *R. tranquebarica* Spreng.

*Centranthera scoparia* Bonati, Not. Syst. 1: 338. 1911, Lecomte, Fl. Gén. Indo-Chine 4: 447. 1927, is only briefly described in comparison with *Razumovia tonkinensis* (Bonati) Merr. It was based on *Balansa* 971 from Ouonbi, Tonkin, and, as suggested by Bonati, it may be merely a habitat form of the preceding species. Until its relationships with *Razumovia tonkinensis* (Bonati) Merr. are more definitely known it seems best not to transfer the specific name to *Razumovia*, for it may ultimately prove not to be distinct from the latter species.

HARVARD UNIVERSITY

## Some Myxophyceae from the Canal Zone<sup>1</sup>

FRANCIS DROUET

(WITH THREE FIGURES)

Through the kindness of Dr. Carroll W. Dodge, I have been permitted to examine a number of specimens of Myxophyceae collected by himself, Dr. J. A. Steyermark, Dr. P. H. Allen, and others on the various expeditions to the Canal Zone and adjacent Panama under the auspices of the Missouri Botanical Garden and the Farlow Herbarium. Most of the material is from subaerial and aerial habitats; one considerable collection dried on mica slips, however, comes from shallow water of Gatun Lake. Dr. G. W. Prescott has obligingly allowed me access to the formalin-preserved material collected by Dr. A. M. Chickering of Albion College and by Dr. G. W. Martin of the State University of Iowa during expeditions to the Canal Zone and Panama in 1934, 1935, and 1936.

Only two papers listing freshwater blue-green algae from the Canal Zone or Panama have been brought to my attention. Ostenfeld & Nygaard in Dansk Bot. Ark. 4 (10), 1925 reported eight planktonic species<sup>2</sup> from Gatun Lake, of which only *Microcystis robusta* was said to occur in abundance. Prescott in Trans. Amer. Microsc. Soc. 55: 501-509, 1936 reported three species from Gatun Lake; it has been my good fortune to examine the material upon which Dr. Prescott's reports were based and to be permitted to treat it critically in the list below.

The species listed here are, with few exceptions, of wide distribution in tropical and temperate regions. Herbaria in which specimens referred to are to be found are indicated by the following abbreviations: *D*, my personal herbarium; *F*, Farlow Herbarium of Harvard University; *Mi*, Herbarium of the University of Michigan; *Mo*, Herbarium of the Missouri Botanical Garden; *N*, Herbarium of the New York Botanical Garden; *Pr*, Herbarium of G. W. Prescott; *T*, Herbarium of Wm. Randolph Taylor; *Y*, Herbarium of Yale University.

*MICROCYSTIS AERUGINOSA* Kütz., Tab. phyc. 1: 6. Tab. 8. 1845-49; Prescott, Trans. Amer. Microsc. Soc. 55: 502. 1936. *Polycystis aeruginosa* Kütz., ibid., 7. 1845-49, *pro synonym. Clathrocystis aeruginosa* Henfr., Trans. Microsc. Soc. London, N. S. 4: 53. Pl. 4, fig. 28-36. 1856, *pro synonym.*—Reported by Ostenfeld & Nygaard (ibid.) in Gatun Lake. See Geitler, Rabenh. Kryptogamen-Fl. 14: 137. 1930. Three collections seen: With

<sup>1</sup> Contribution from the Osborn Botanical Laboratory of Yale University.

<sup>2</sup> *Microcystis robusta* (Clark) Nygaard, *M. aeruginosa* Kütz., *M. pulverea* DeToni (?), *Oscillatoria sancta* Kütz., *O. formosa* Bory, *Lyngbya major* Menegh., *Anabaena* sp., and *Hapalosiphon* sp.

and sub nom. *Anabaena unispora*, Gatun Lake, near Barro Colorado Island, A. M. Chickering, July 1934 (*D, F, Pr, Y*); Barro Colorado Island, A. M. Chickering, 5 July 1936 (*D, Pr, Y*), 4 Aug. 1936 (*D, F, N, Pr, Y*).

GLOEOCAPSA GIGAS W. & G. S. West, Journ. Linn. Soc. Bot. **30**: 276. Pl. 16, fig. 11–13. 1894. *Anacystis gigas* Gardn., Mem. New York Bot. Gard. **7**: 15. 1927, *pro synonym*.—This is an aerial form apparently of wide distribution in the tropics. The Wests described it originally from St. Vincent in the West Indies, where it was found growing 'on damp wall of dam, Sharp's River' (not 'in einem Fluss,' as Geitler has mistakenly transcribed this in Rabenh. Kryptogamen-Fl. **14**: 192. 1930). Wille in Denkschr. Math.-Natur. Kl. k. Akad. Wiss. Wien **91**: 7. Taf. 1, fig. 5–8. 1914 later reported it from rocks on the island of Savaii, Samoa. Gardner (loc. cit.) recently showed it to be a form of rather general distribution in aerial situations in Puerto Rico. I have had the opportunity of seeing only the Puerto Rican collections discussed by Gardner, other than the two collections from the Canal Zone reported here: Moist lime bluff, near Salamanca Hydrographic Station on the gorge of the R. Pequení, Dodge, Steyermark & Allen 16972, 16975, 14 Dec. 1934 (*D, Mo, Y*).

APHANOTHECE PALLIDA (Kütz.) Rabenh., Kryptogamen-Fl. Sachsen, **76**. 1863. *Palmella pallida* Kütz., Tab. phyc. **1**: 11. Tab. 14, fig. LV. 1845–49.—I am unable to detect differences between the colonies as represented in Rabenhorst, Algen 1831 (*F, N*), and those in the one collection from Gatun Lake: Among other algae among the floating islands, north arm of Gigante Bay, C. W. Dodge, 9 Aug. 1925 (*D, Mo*).

CHROOCOCCUS TURGIDUS (Kütz.) Näg., Gatt. einzell. Alg., **46**. 1849. *Protococcus turgidus* Kütz., Tab. phyc. **1**: 5. Tab. 6. 1845–49. *C. limneticus* of Prescott, Trans. Amer. Microsc. Soc. **55**: 502. 1936, not Lemm.—The material here is similar to that distributed in Wittrock & Nordstedt, Alg. exs. 100, 699, and 799 (*N*). See Boye Petersen, Bot. Icel. **2**: 263 (1928), and Geitler, Rabenh. Kryptogamen-Fl. **14**: 228. 1930. Colonies are not abundant in the two collections from Gatun Lake: Among other algae among the floating islands Gigante Bay, C. W. Dodge, 9 Aug. 1925 (*D, Mo, Y*); with and sub nom. *Anabaena unispora*, Gatun Lake, near Barro Colorado Island, A. M. Chickering, July 1934 (*D, F, Pr, Y*).

ANABAENA UNISPORA Gardn., Mem. New York Bot. Gard. **7**: 59. Pl. 12, fig. 8. 1927; Prescott, Trans. Amer. Microsc. Soc. **56**: 502. Pl. LXV, fig. 12–14. 1936.—This alga grows in flocculent clumps up to 1.5 cm. in diameter, floating free in the water or entangled in masses of other algae. The trichomes are straight or somewhat flexuous, mostly lying parallel with each other, and rather compactly so in the older masses. The protoplasm is coarsely granular; there is evidence that at least some of these

granules are pseudovacuolar in nature. Gardner figures the spore as simply ovoid; though in the type specimen in the Herbarium of the New York Botanical Garden many of the spores are of this shape, the majority is long-ovoid or ellipsoidal and conspicuously narrowed at either point of attachment (Fig. 1). Prescott has figured an immature spore. In the future

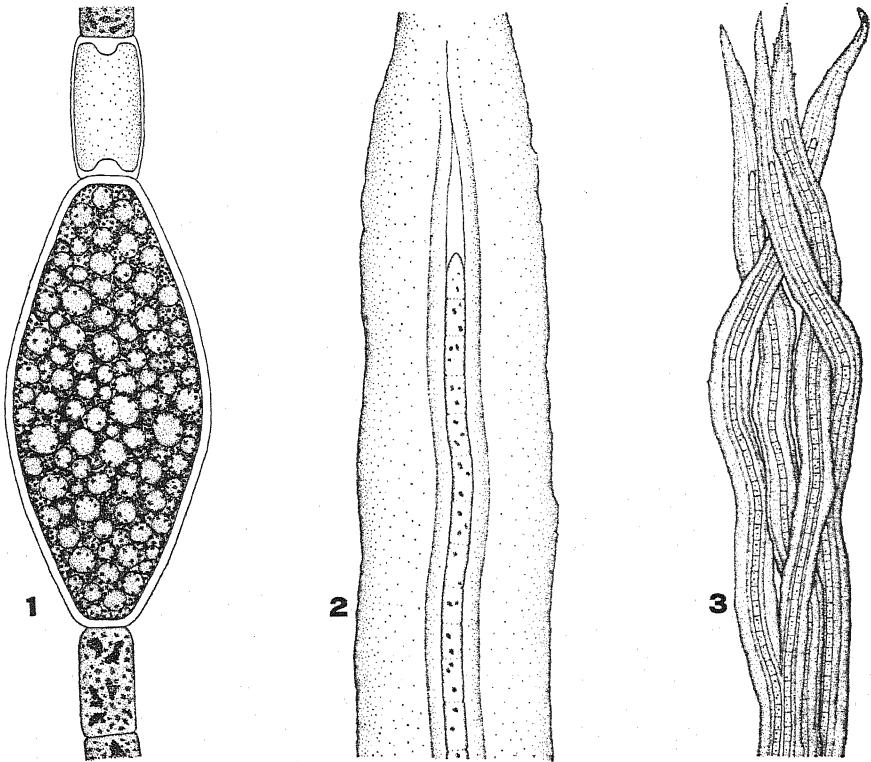


Fig. 1. Detail of mature spore, heterocyst, and vegetative cells from the type specimen of *Anabaena unisporea* Gardn.  $\times 2000$ .

Fig. 2. Portion of filament with included trichome from the type of *Schizothrix violacea* Gardn.  $\times 1500$ .

Fig. 3. Upper portion of a fascicle of filaments of *Schizothrix violacea* from Dodge, Steyermark & Allen 16971 from the Canal Zone.  $\times 200$ .

it will probably become necessary to synonymize the name *A. unisporea* Gardn. with *A. Volzii* Lemm., Abh. Nat. Ver. Bremen 18: 153. Taf. IX, fig. 4, 5, 20. 1906, described from Singapore and Java. I refrain from using the latter name here because I have not had the opportunity to compare the types of the two species. Specimens seen: MICHIGAN: McDonald



Lake, Yankee Springs, Hastings, *G. T. Velasquez* 15, 4 Aug. 1936 (*Velasquez, D, F, Mi, Y*). PUERTO RICO: in a pool near the Park, Santurce, *Wille* 49a (TYPE in Herb. New York Bot. Gard.), 49c, 61d, 25 Dec. 1914 (*N*). CANAL ZONE: Among the floating islands, Gigante Bay, *C. W. Dodge*, 9 Aug. 1925 (*D, Mo, Y*); Gatun Lake, near Barro Colorado Island, *A. M. Chickering*, July 1934 (*D, F, Pr, Y*).

SCYTONEMA COACTILE Mont. ex Born. & Flah., Ann. Sci. nat. VII Bot. 5: 90. 1887.—Most of the trichomes in the very abundant material from Gatun Lake measure 12–18 $\mu$  in diameter, but those produced under sub-aerial conditions in the plant masses measure as little as 7.5 $\mu$  in diameter. One collection: Among the floating islands, Gigante Bay, *C. W. Dodge*, 9 Aug. 1925 (*D, F, Mo, Y*).

SCYTONEMA STUPOSUM (Kütz.) Born. ex Born. & Flah., Ann. Sci. nat. VII Bot. 5: 92. 1887. AUTHENTIC MATERIAL: Rabenhorst, Algen 2339 (*F*).—One collection: On dripping limestone cliff, drowned forest along R. Chagres between junction with R. Pequení and with R. Indio, *Steyermark & Allen* 16816, 5 Dec. 1934 (*D, Mo*).

SCYTONEMA OCELLATUM Lyngb. ex Born. & Flah., Ann. Sci. nat. VII Bot. 5: 95. 1887. AUTHENTIC MATERIAL: Erbar. critt. ital., ser. II, 1044 (*F*).—One collection: Moist limestone bluff near Salamanca Hydrographic Station on the gorge of the R. Pequení, *Dodge, Steyermark & Allen* 16973, 14 Dec. 1934 (*D, Mo*).

SCYTONEMA VARIUM Kütz. ex Born. & Flah., Ann. Sci. nat. VII Bot. 5: 97. 1887.—I place the following specimens under this name rather than under *S. Hofmannii* because of the gelatinous sheaths and the short cells and heterocysts: Along Wheeler trail, Barro Colorado Island, *Dodge* 3800, 21 July 1925 (*D, Mo, Y*); Barro Colorado Island, *O. Shattuck*, 1931 (*D, Mo*).

SCYTONEMA HOFMANNII Ag. ex Born. & Flah., Ann. Sci. nat. VII. Bot. 5: 97. 1887; Bornet & Thuret, Notes algol. 2: 138, 148. Tab. XXXV. 1880. AUTHENTIC MATERIAL: Rabenhorst, Algen 2464 (*F*). The three collections listed approach the var. SYMPLOCOIDES (Reinsch) Born. & Flah., *ibid.*, 99 (*non sensu* Geitler, Rabenh. Kryptogamen-Fl. 14: 773. 1932), as represented in Rabenhorst, Algen 1923 (*F*), though old sheaths are seen with a yellowish-brown color. The collections come from trunks of trees: Along Barbour trail, Barro Colorado Island, *Dodge* 3674, 4 July 1925 (*D, Mo, Y*); on bark and orchid roots, Balboa, *G. W. Martin* 2032, 22 June 1935 (*D, Pr*).

SCYTONEMA ALATUM (Berk.) Borzi ex Born. & Flah., Ann. Sci. nat. VII Bot. 5: 110. 1887. *Petalonema alatum* Berk. ex Geitl., Cyanophyceae, 264. Fig. 316. 1925. AUTHENTIC MATERIAL: Rabenhorst, Algen 2183 (*N*).

—See Geitler, Rabenh. Kryptogamen-Fl. **14**: 788 ff. 1932. Specimens seen: On dripping limestone cliff, drowned forest along R. Chagres between junction with R. Pequení and with R. Indio, *Steyermark & Allen 16811*, 5 Dec. 1934 (*D, Mo, Y*); moist lime bluff near Salamanca Hydrographic Station on the gorge of the R. Pequení, *Dodge, Steyermark & Allen 16975*, 14 Dec. 1934 (*D, Mo, Y*).

*SCHIZOTHRIX CHALYBEA* (Kütz.) Gom., Ann. Sci. nat. VII Bot. **15**: 319. Pl. IX, fig. 3–5. 1892; Collins in Britton & Millspaugh, Bahaman Flora, 624. 1920.—From the data on and the appearance of herbarium specimens, this species appears usually to inhabit moist limestone. The following specimens seen indicate the geographic distribution: BAHAMA ISLANDS: on limestone cliffs, Nassau, New Providence, *A. E. Wight*, 4 Jan. 1905 (*F*); opposite Adelaide, 'on mud surfaces,' New Providence, *Brace 9421, 9423*, 12 May 1918 (*D, N*). MEXICO: Orizaba, *F. Müller*, 1853 (ISOTYPE annotated by Gomont, *F*). CANAL ZONE: Moist limestone bluff near Salamanca Hydrographic Station on the gorge of the R. Pequení, *Dodge, Steyermark & Allen 16974*, 14 Dec. 1934 (*D, Mo*).

*SCHIZOTHRIX THELEPHOROIDES* (Mont.) Gom., Ann. Sci. nat. VII Bot. **15**: 319. Pl. X, fig. 1–4. 1892.—Two collections: On moist earth, sabanas along drowned R. Azote Caballo, *Dodge, Steyermark & Allen 16864, 16871*, 7 Dec. 1934 (*D, Mo, Y*).

*Schizothrix violacea* Gardn., descr. emend. *S. violacea* Gardn., Mem. New York Bot. Gard. **7**: 52. Pl. 11, fig. 99. 1927. Fila elongata, subrigida, parce tortuosa, pseudo-ramosa pseudo-ramis adpressis, saepe in fasciculos repentis aggregata; vaginis violaceis (in maturitate nigro-violaceis) ad apices raro hyalinis vel pallide violaceis, firmis, crassis, lamellosis, ambitu frequenter erosis interdum fimbriatis, apice longe attenuatis et acuminatis, chlorozincico iodurato caerulescentibus; trichomatibus pallide aerugineis, intra vaginam paucis, remotis, parallelis, in ramis saepius singulis, ad genicula leviter constrictis,  $2\mu$  ad  $2.5\mu$  crassis; articulis diametro trichomatis usque triplo longioribus, rarius subquadratis,  $2\mu$  ad  $7\mu$  longis; protoplasmate sparsim grosse-granuloso; dissepimentis haud conspicuis, haud granulatis; cellula apicali obtuse-conica, sine calyptra (v. s.). Fig. 2 and 3. On moist limestone: PUERTO RICO: growing among other Myxophyceae on limestone, Arecibo to Utuado, *Wille 1416g*, 4 Mar. 1915 (TYPE in Herb. New York Bot. Gard.). CANAL ZONE: With other Myxophyceae on moist lime bluff near Salamanca Hydrographic Station on the gorge of the R. Pequení, *Dodge, Steyermark & Allen 16971*, 14 Dec. 1934 (*D, Mo, Y*).—The type material from Puerto Rico contains mostly very short filaments, as Gardner has indicated, though long and branched filaments as described above are also present. The Canal Zone

material illustrates the plant mass in a far more mature state of development. The violet sheaths distinguish *S. violacea* from all other members of the genus; this species should find a place in the section Chromosiphon in the vicinity of *S. Heufleri* Grun. ex Gom. and *S. Braunii* Gom.

SYMPLOCA DUBIA (Nag.) Gom., Ann. Sci. nat. VII Bot. 16: 115. 1892. AUTHENTIC MATERIAL: Rabenhorst, Algen 593 (*T*).—The abundant material comes from a single station and represents every stage in the development of the plant mass: Dripping limestone cliffs, drowned forest along R. Chagres between junction with R. Pequení and with R. Indio, *Steyermark & Allen 16812, 16813, 16814, 16817, 16818, 16819*, 5 Dec. 1934 (*D, Mo, Y*).

LYNGBYA LAGERHEIMII (Möb.) Gom., Ann. Sci. nat. VII Bot. 16: 147. Pl. IV, fig. 6 & 7. 1892.—One specimen: On Chara, Gatun Lake, *D. P. Curry 13*, 11 June 1934 (*N*).

LYNGBYA OCHRACEA (Kütz.) Thur. ex Gom., Ann. Sci. nat. VII Bot. 16: 149. 1892. AUTHENTIC MATERIAL: Rabenhorst, Algen 58 (*F*), 2333 (*F*).—One collection: El Valli, *A. M. Chickering*, 16 July 1936 (*D, F, N, Pr, Y*).

PHORMIDIUM PAPYRACEUM (Ag.) Gom., Ann. Sci. nat. VII Bot. 16: 174. Pl. V, fig. 3 & 4. 1892. AUTHENTIC MATERIAL: Rabenhorst, Algen 2089 (*F*); Wittrock & Nordstedt, Alg. exs. 776a & b (*F*); Hauck & Richter, Phyk. univ. 233 (*F*).—One collection from Gatun Lake: Among other algae among the floating islands, north arm of Gigante Bay, *C. W. Dodge*, 9 Aug. 1925 (*D, Mo*).

OSCILLATORIA RUBESCENS DC. ex Gom., Ann. Sci. nat. VII Bot. 16: 204. Pl. VI, fig. 6 & 7. 1892.—The plant here seems indistinguishable from this species as represented in the specimen distributed from the Herb. Bornet: SWITZERLAND: Lac de Morat, *M. Chaillot*, 1825 (*F*). Planktonic in Gatun Lake: Panama Canal, Barro Colorado Island, *A. M. Chickering*, 1 July 1936 (*D, F, N, Pr, Y*).

OSBORN BOTANICAL LABORATORY,  
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## Lowland vegetation of Sinaloa

FORREST SHREVE

(WITH THREE FIGURES)

It is impossible to gain a thorough knowledge of the botanical features of a great natural region without knowing something about the areas adjacent to it. Light is thrown on every aspect of the phytogeography and ecology of an extended formation by investigation of its plants and its social and habital features as they exist under the slightly different conditions of nearby formations.

In a recent paper<sup>1</sup> the writer has very briefly described the boundaries of the Sonoran Desert, the character of its vegetation and the aims of work now in progress on it. The Sonoran Desert is a region of strong biological unity, with a highly distinctive flora, and a number of ecological features which serve collectively to distinguish it from adjacent regions and from the other desert areas of North America. Five types of vegetation are found around the periphery of the Sonoran Desert: chaparral, microphyllous desert (Mojave Desert), desert grassland, evergreen oak woodland (encinal), and thorn-forest. The writer has published descriptions of the transitions from the Sonoran Desert to thorn-forest<sup>2</sup> and to chaparral.<sup>3</sup>

In recent work the transition from desert to thorn-forest and the thorn-forest itself have again been examined. The lowlands of the extreme southern end of Sonora and the entire state of Sinaloa are occupied by thorn-forest and constitute the most important one of the five encircling regions. Far less is known about the thorn-forest than the other regions, but it is the most important one of them in its contributions toward a knowledge of the history of the Sonoran Desert. In the thorn-forest are found many convincing or suggestive pieces of evidence as to the derivation of some of the desert species, the origin of some of the structural and physiological peculiarities of desert plants, and the beginnings of some of the features of vegetational structure and consociation which it manifests.

The Mexican state of Sinaloa extends from the crest of the Sierra Madre Occidental down to the shores of the Pacific Ocean, a distance varying from 80 to 240 km. (50 to 150 mi.). The southern end of the state is in the tropical zone and the northern end 4° above the Tropic of Cancer. Nearly equal areas are occupied by a continuous coastal plain and by the

<sup>1</sup> Shreve, Forrest. The plant life of the Sonoran Desert. *Sci. Mo.* 42: 195-213. 1936.

<sup>2</sup> Shreve, Forrest. Vegetation of the northwestern coast of Mexico. *Bull. Torrey Club* 61: 373-380. 1934.

<sup>3</sup> Shreve, Forrest. The transition from desert to chaparral in Baja California. *Madroño* 3: 257-264. 1936.

foothills and slopes of the mountains. The plain is crossed by seven large rivers with broad alluvial valleys. The writer has examined the thorn-forest from the Rio Yaquí, in southern Sonora, to the Rio Union, in southern Sinaloa, a distance of 640 km. (400 mi.). The formation extends far to the south along the Pacific coast, but doubtless with many changes in composition and physiognomy.

A map and brief description of the vegetation of northwestern Mexico have been published by Brand.<sup>4</sup> He designates the vegetation of the coastal plain and lower mountain slopes as semi-arid scrub.

The coastal plain exhibits great uniformity in vegetation throughout the northern half of Sinaloa, and gradual change on going south through the lower end of the state. The belt immediately along the coast is more arid than the interior and poorer and more open in its vegetation. The flood plains are largely devoted to vast fields of sugar, garbanzo, tomatoes and corn. Their natural vegetation is more luxuriant than that of the uplands and their flora includes many tropical plants. The vegetation of the hills which are scattered over the plain is commonly very similar to that of the plain. In the lowlands of Sinaloa the coastal plain type of thorn-forest, locally called "montaña," greatly predominates in area over the vegetation characterizing the flood-plains, the extreme coast and the hills. There has been very little disturbance of the natural condition of the montaña. Agricultural development has been favored by the flood-plains, grazing has been limited by the scarcity of forage grasses, and wood for construction and fuel has been secured from the trees of the flood-plains and foothills.

The thorn-forest has an ameliorated type of desert climate. The temperatures are almost continuously favorable to growth. The rainfall is higher than in any parts of the Sonoran Desert but is like that of the desert in having a very uneven seasonal distribution. At Mazatlan, in the southern end of Sinaloa, the mean annual rainfall (1889-1936) is 767.8 mm. (30.20 in.). During July, August and September there are heavy rains which yield 76.4% of the annual total. From November to May inclusive the mean rainfall is only 78.9 mm. (3.11 in.). For March, April, May and June it is 38.0 mm. (1.49 in.), being only 7.7 mm. (.30 in.) for the first three of these months. The occurrence of eight consecutive months which are dry, and the last four of them very dry, serves to give the moisture conditions a close relation to those of the desert. Biseasonal rainfall is characteristic of the northern part of the Sonoran Desert, but on going south the winter

<sup>4</sup> Brand, Donald D. Notes to accompany a vegetation map of northwest Mexico. Univ. New Mex. Bull. 280. 1936.

precipitation becomes more and more uncertain and much smaller in amount. At Mazatlan the mean precipitation for the five months from November to March inclusive is only 10.3% of the annual total, and the curve of monthly distribution shows a summer maximum with no winter sub-maximum. On rare occasions the monthly precipitation of one of the winter months may be 100 mm. (4 in.) or more, there having been four such occurrences since 1880.

It has been shown by the writer<sup>5</sup> for the Tucson region that the heavy runoff accompanying the torrential summer rains makes them less effective in replenishing soil moisture than are the gentler and more prolonged

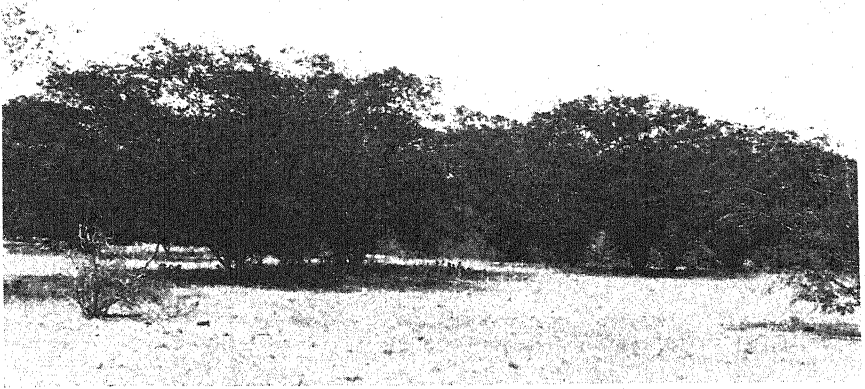


Fig. 1. Northern fringe of the thorn-forest in southern Sonora. Open stand of *Acacia cymbispina* with sparse undergrowth.

winter rains. It seems highly probable that the heavy summer rains of Sinaloa do not result in as great an increase in available soil moisture as their amount would suggest. The copious fall, however, spread over a period of three months, gives the vegetation a favorable period which lasts long enough for the entire life cycle of herbaceous plants and long enough for flowering, maturing of seeds and considerable growth on the part of the perennials. For the continuous development of the vegetation the long series of dry months is strongly deterrent and results in the xeric features which make the thorn-forest akin to the desert.

Thorn-forest differs from desert in the greater stature of the dominant

<sup>5</sup> Shreve, Forrest. Rainfall, runoff and soil moisture under desert conditions. Ann. Assn. Amer. Geogs. 24: 131-156. 1934.

plants, in their universally greater density of stand, and in the almost unbroken occurrence of a subordinate stand or layer of shrubs. There is also an approach toward uniformity of vegetative type, which is in strong contrast to the diversity found in the Sonoran Desert. The most pronounced xeric features of the thorn-forest are its prevalent height, which rarely exceeds 7 to 8 m. (23 to 26 ft.), and is very often less, its scanty and open canopy, the strong predominance of trees with small leaves or very small leaflets, the occurrence of cacti, and the great difference between the vegetation of the general surface and that of the flood-plains and margins of streamways.

The trend toward uniformity consists in the preponderance of trees, the relatively unimportant rôle of the succulents, the reduction of shrubs to a secondary place as undergrowth, and the absence or infrequency of the desert types represented by *Holacantha*, *Dalea spinosa*, *Yucca*, *Agave*, *Dasyllirion*, *Atriplex* and *Bebbia*. Although thorn-forest has a smaller range of plant types than desert, it is noteworthy that the trees of the former region show a great diversity in size, mode of display of foliage, seasonal behavior of leaves, character of trunk and form of crown. A few vegetative types appear in the thorn-forest which are absent or unimportant in the desert. Palms are locally abundant but chiefly in the flood-plains. Terrestrial bromeliads and epiphytic species of *Tillandsia* are abundant in southern Sinaloa. Both woody and herbaceous vines are far more abundant than they are in any but the most favorable habitats in the southern part of the Sonoran Desert.

The semi-arid climate of the thorn-forest is intimately related to the preponderance of trees with compound leaves which have leaflets less than 25 sq. mm. in area (*Acacia cymbispina*, *Lysiloma divaricata*, *Lysiloma microphylla*, *Prosopis glandulosa*, *Pithecolobium sonorae*, *Eysendardtia orthocarpa*, *Acacia Farnesiana*, *Acacia pennatula*). Trees are also frequent which have compound leaves with leaflets larger than 25 to 50 sq. mm. in area (*Cassia atomaria*, *Lonchocarpus megalanthus*, *Caesalpinia platyloba*, *Guaiacum Coulteri*, *Diphysa suberosa*). South of central Sinaloa there is a marked increase in the abundance of trees with the latter type of leaf. The number of trees with simple leaves more than 5 sq. cm. in area is small throughout the montaña of Sinaloa. The commonest of these are the ever-green *Zizyphus sonorensis* and the deciduous *Ipomoea arborescens*, as well as *Jatropha cinerea*, *Bunchosia Palmeri*, *Cordia sonorae*, *Ficus petiolaris* and *Sapium lateriflorum*.

The majority of the common thorn-forest trees are either wholly deciduous in winter or else lose about half their leaves and retain the rest in a condition in which their transpiration, respiration and photosynthesis

are probably at a low ebb. The lack of complete autumnal defoliation of such trees is largely due to their very general failure to develop an abscission layer at the base of the petiole.



Fig. 2. Thorn-forest between Culiacan and Altata, 25 km. from the coast in central Sinaloa. *Ipomoea*, *Zizyphus* and *Pachycereus* in center, *Acacia* on right.

Fig. 3. Thorn-forest on low hills near Villa Union, in southern Sinaloa.

The vegetation of the thorn-forest in Sinaloa is dominated by *Acacia cymbispina* ("bínolo"), which everywhere forms from 60% to 90% of the stand in the lowland region. It is a tree with one or several slender



trunks arising from a common root, and an open top which spreads gradually to a flat crown. The slender branches and finely cut leaves are symmetrically distributed throughout the tree. The shade cast by the foliage is very light. The height of the tree varies from 5 to 8 m. (16 to 26 ft.). The most distinctive character is the light gray stipular spines, about 5 cm. in length, which are split along the top so as to resemble a minute canoe.

In northern Sinaloa *Acacia cymbispina* forms open park-like groves but in central and southern Sinaloa it grows in a thick stand. Its relative abundance is less on the steep or high slopes of isolated hills or the foothills of the mountains, and is very much less on the flood-plains. Its abundance does much to determine the general level of the thorn-forest canopy, but a number of common trees usually exceed it in height.

The arborescent flora of Sinaloa probably comprises 250 species, at least half of which are found in the lowlands. The most common associates of *Acacia* in the upland of the coastal plain are the following. Trees mainly confined to the northern or southern parts of the state are so indicated.

<i>Ipomoea arborescens</i>	<i>Bauhinia longiflora</i>
<i>Pachycereus pecten-aboriginum</i>	<i>Ceiba acuminata</i>
<i>Cassia atomaria</i>	<i>Jatropha cinerea</i>
<i>Zizyphus sonorensis</i>	<i>Acacia pennatula</i>
<i>Pithecolobium sonorae</i>	<i>Elaphrium Simaruba</i> S
<i>Caesalpinia platyloba</i>	<i>Guazuma ulmifolia</i>
<i>Lonchocarpus megalanthus</i> S	<i>Guaiacum Coulteri</i>
<i>Jatropha cordata</i>	<i>Sapium lateriflorum</i> S
<i>Cassia emarginata</i>	<i>Haematoxylon brasiletto</i>
<i>Cercidium Torreyanum</i> N	<i>Jatropha curcas</i> S
<i>Lysiloma divaricata</i>	<i>Crescentia alata</i> S
<i>Ichthyomethia mollis</i> N	<i>Cercidium sonorae</i>

The flora of the Sonoran Desert includes a considerable number of small trees, which are important in the vegetation of hills, mountain slopes, coarse outwash slopes and flood-plains. The total area in which they are abundant is, however, greatly exceeded by the broad stretches in which shrubs and small woody perennials are the dominant plants. The thorn-forest is probably richer than the desert in the number of its shrubby species, and much of it is richer in the number of individuals per unit area. Nevertheless the thorn-forest shrubs are a secondary element of the vegetation, finding space only in the light shade of *Acacia* and its associates and forced to compete with the trees for water supply. The widely different status of the shrub in desert and thorn-forest has doubtless been an important factor in bringing about or maintaining the strong difference which

now exists between the lists of characteristic shrubs found in the two formations.

The shrubs of the Sonoran Desert fall into two classes, which are not sharply separable but are more easily distinguished than are trees and shrubs. The first includes species with hard wood, sparse or moderate branching, and determinate growth, including *Larrea tridentata*, *Acacia Greggii*, *Condalia spathulata*, *Simmondsia californica*, *Jatropha cardiophylla*, *Mimosa laxiflora*, and *Caesalpinia gracilis*. The second class embraces shrubs with soft wood, rich branching, and indeterminate growth, and includes nearly all of the perennial members of several genera which are of great importance in the Sonoran Desert, notably *Atriplex*, *Viguiera*, *Encelia*, *Franseria*, *Lippia*, *Eriogonum*, *Brickellia*, and *Aplopappus*.

The first type of shrub is represented in the thorn-forest by a large number of species in the genera *Cassia*, *Caesalpinia*, *Acacia*, *Croton*, *Karwinskia*, *Mimosa*, *Lysiloma*, *Bauhinia*, *Acalypha* and many others. Nearly all of the shrubs of this type found in the Sonoran Desert belong to genera which are well represented in the thorn-forest, both with respect to number of species and abundance of individuals. Distributional evidence indicates that this type has spread from the thorn-forest into the desert and the desert mountain ranges. Plants of the second type are common in all four of the North American deserts, and are probably of desert origin. They are very poorly represented in northern Sinaloa and are absent in the southern end of the state. The single species of this type which has been able to invade the thorn-forest with success is *Franseria cordifolia*, a plant of desert affinities which is very abundant in northern Sinaloa.

Following are listed some of the most common and characteristic shrubs of the lowlands of Sinaloa. The first five are particularly abundant.

<i>Croton alamosanus</i>	<i>Croton sonorae</i>
<i>Franseria cordifolia</i>	<i>Hyptis Emoryi</i>
<i>Caesalpinia gracilis</i>	<i>Lagascea decipiens</i>
<i>Karwinskia Humboldtiana</i>	<i>Parthenium Stramonium</i>
<i>Cassia biflora</i>	<i>Lippia Palmeri</i>
<i>Lantana involucrata</i>	<i>Cassia Wislizeni</i>
<i>Carlowrightia californica</i>	<i>Turnera diffusa</i>
<i>Randia Thurberi</i>	<i>Justicia mexicana</i>
<i>Phaulothamnus spinescens</i>	<i>Iresine Hartmannii</i>
<i>Cassia occidentalis</i>	<i>Lippia Berlandieri</i>
<i>Vallesia glabra</i>	<i>Colubrina glabra</i>
<i>Diphysa racemosa</i>	<i>Mascagnia macroptera</i>

In the Sinaloan thorn-forest cacti are far less important in the composition of the vegetation than they are in the Sonoran Desert. There are few

habitats in which they dominate the appearance of the landscape. The most abundant and conspicuous species is *Pachycereus pecten-aboriginum*, which occurs in all but the heaviest stands of the montaña but is often absent over areas several kilometers wide. Unlike *Carnegiea* and *Pachycereus Pringlei* its local distribution bears no relation to the topography. The slender *Rathbunia alamosana* and the erect dark green *Opuntia fuliginosa* are frequent in occurrence but never form large colonies. The low much-branched *Opuntia pubescens* is found in very open stands of *Acacia* and is most abundant in the small openings in the northern edge of the thorn-forest. *Lemaireocereus Thurberi* plays an unimportant part in the vegetation of the lowlands. Near the coast *Opuntia tomentosa* is frequent, forming erect plants 6 to 8 m. (19 to 26 ft.) high, and *Acanthocereus occidentalis* sprawls about in thickets and openings. Throughout the lowlands the various species of *Ferocactus*, *Mammillaria* and *Echinocactus* are infrequent, except in the low and open stands of montaña near the coast. In dense thickets a semi-scandent *Pereskiaopsis* is often found. It is significant that the common cacti of the thorn-forest are all shade-enduring forms. Only two of them (*Lemaireocereus Thurberi*, *Opuntia Thurberi*) are found in the open desert of central Sonora. There are 23 species of *Opuntia* and 10 other cacti which are abundant in northern Sonora but absent from Sinaloa.

A single genus of *Euphorbiaceae* with succulent stem is abundantly represented in the thorn-forest by *Pedilanthus rubiginosus*. Its poorly branched stems reach a height of 2 to 3 m. and bear leaves on the growth of the season. In central Sinaloa the *Fouquieriaceae* are represented only by infrequent individuals of *Fouquieria Macdougalii*.

The Sinaloan thorn-forest is rich in both annual and perennial herbaceous plants. The conditions for perennation are so good that it is not always possible to distinguish readily between ephemerals and root perennials. The summer months are the season of greatest development for herbaceous plants and many of them persist and continue activity until January, or later, depending on their habitat and the occurrence of rain. There are few, if any, ephemerals which are active only in the winter. The position of herbaceous plants in the vegetation is determined by the seasonal distribution of rainfall and by the character of the habitats that are available to them. Germination is undoubtedly confined to the early days of the rainy season. Only in the northern part of the thorn-forest are there large openings such as are thickly carpeted with ephemerals in the desert. Elsewhere they grow perforce in the light shade of *Acacia* or in the heavier shade of trees and shrubs. Under the heaviest stands of perennials,

where a cane knife is essential to progress, there are few small herbaceous plants. In places where shrubbery is sparse the herbaceous plants are very abundant.

#### SUMMARY

The lowland half of the Mexican state of Sinaloa has a semi-arid climate, with abundant rainfall in the three summer months and little or none in the other months. The vegetation is an open or closed stand of trees from 5 to 8 m. (16 to 26 ft.) in height, dominated by *Acacia cymbispina*, numerous other small-leaved trees and a few large-leaved ones. Shrubs are abundant as undergrowth. Cacti are well represented but not abundant.

The Sinaloan thorn-forest is one of the plant formations bordering the Sonoran Desert. The floras of the two are closely related but the dominant species are distinct. The desert type of shrub, or half-shrub, exemplified by *Atriplex* and *Franseria*, is almost unrepresented in the thorn-forest, and the species of cacti which grow in the open in the desert are absent. There is some evidence that the thorn-forest has contributed the ancestral stock of numerous desert trees and shrubs.

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# INDEX TO AMERICAN BOTANICAL LITERATURE 1934-1937

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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